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P. L. FOREY

BULLETIN OF
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GEOLOGY Supplement 10
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By PETER L. FOREY*

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SYNOPSIS

The skeletons of the Recent elopiform fishes (*Elops, Tarpon, Megalops, Pterothrissus, Albula*) are described, and all fossil genera thought to be correctly placed in the Elopiformes are reviewed and compared with the living forms. From the descriptions it is concluded that the classification of the Elopiformes given by Greenwood *et al.* (1966) reflects the phylogeny of this group. A new family, the Osmeroididae, based on the Cretaceous genus *Osmeroides*, is included in the suborder Albuloidei as the basal family of that suborder. The Osmeroididae provide a link between the Elopoidei and the more specialized Albuloidei. Primitive and advanced features of the Elopiformes are discussed together with individual discussions of the contained suborders. Three new fossil genera are established : *Davichthys, Protarpon* and *Lebonichthys*. The relationship of the Elopiformes with other basal teleost groups is considered and it is concluded that although no relationship exists with the Clupeomorpha and Osteoglossomorpha within the Teleostei, the possibility of a relationship with the Euteleostei cannot be ruled out.

I. INTRODUCTION

THIS work is a taxonomic revision of the order Elopiformes Greenwood *et al.* (1966). The Elopiformes are a group of primitive teleosts related to the highly specialized Anguilliformes and Notacanthiformes by virtue of the fact that members of all three orders show a leptocephalus larval stage in their life history. The elopiforms are represented in the Recent fauna by a handful of genera ; *Elops, Megalops, Tarpon, Albula, Dixonina* and *Pterothrissus*. There are more fossil genera, found from the Upper Jurassic onwards. Woodward (1901) lists eighteen genera while Romer (1966) includes some forty-six in the Elopiformes. Although many of these fossil forms do not appear to be members of the Elopiformes, it remains true that the order is largely constituted by extinct genera.

Most fossil elopiforms are known from Upper Cretaceous deposits and were originally described in several faunal works. The more important of these works are those of Agassiz (1833–1844) in which forms from several localities were dealt with ; Dixon (1850) described the English Chalk species ; Pictet (1850), Pictet & Humbert (1866), Davis (1887) and Hay (1903) described those from the Lebanon. Marck (1858, 1863) noted forms from the Westphalian Chalk and Cope (1872), Loomis (1900) and Stewart (1898) were concerned with those from the Kansas Chalk. This earlier work was synthesized by Woodward (1901) who went on to deal extensively (1907, 1908) with the English Chalk fauna. In more recent years d'Erasmo (1946) has published on the Upper Cretaceous fauna from Comen, Yugoslavia, Arambourg (1954) has described elopiforms from the Cretaceous of Morocco and a revision of the Westphalian fauna has been undertaken by Siegfried (1954).

Important work on the anatomy and taxonomy of certain fossil genera has been published by Nybelin (1967b) and Gaudant (1968) for *Anaethalion*, and by Goody (1969a) for *Sedenhorstia*. Recent elopiforms have received attention in faunal works by Barnard (1925), Fowler (1936), Okada (1960) and Hildebrand (1963). Finally, important contributions to the anatomical features of the Recent forms have been made by Ridewood (1904), Hollister (1936, 1939), Nybelin (1956, 1967a, 1971) and Greenwood (1970a). Apart from these specific references the genera *Elops* and *Megalops* have often been referred to in papers concerned with phylogeny and comparative anatomy.

The starting point of the work was taken from Woodward (1901), who recognized the two families Elopidae and Albulidae. Woodward (1901) used a key to divide the Elopidae into two assemblages, later termed the ' elopine ' and ' spaniodontine ' groups by Dunkle (1940). This basic division of the elopids was based on the condition of the parietals, medially united in the ' elopines ' and separated by the supraoccipital in the ' spaniodontines '. During the course of this revision it became apparent that many of the ' spaniodontine ' genera together with two from the ' elopine ' group represent an assemblage distinct from the Elopiformes. These genera (*Notelops, Rhacolepis, Pachyrhizodus, Thrissopater, Esocelops* and possibly *Spaniodon* and *Thrissopteroides*) differ from elopiform fishes in many important details of the snout, the otic region of the neurocranium, the jaws, the infraorbital series, the vertebral column and caudal skeleton, which show that these genera are more correctly placed with the euteleostean fishes. They will be dealt with in a later publication.

Of the genera included by Woodward in the family Albulidae only *Albula* and *Istieus* are retained here. *Chanoides, Chanos, Prochanos* and probably *Ancylostylos* are all interrelated and their affinities lie with the Gonorynchiformes. *Ananogmius* White & Moy-Thomas (*nom. subst.* for *Anogmius* Cope, 1877) shows many cranial and caudal features indicating that it is a member of the osteoglossomorph family Plethodontidae (for features of the plethodonts see Bardack 1965 and Patterson 1967c).

It has been impossible to examine at first hand all genera which have at one time or another been referred to the Elopiformes. Where relevant, comments are included on these unexamined forms, but the many records of isolated otoliths and scales have been omitted because of their debatable value in a work of this nature.

Greenwood *et al.* (1966), writing from a neontological point of view, proposed a classification for the Elopiformes which is substantiated here. The Elopiformes are separable into two rather different suborders, the Elopoidei Jordan (1923) and the Albuloidei Greenwood *et al.* (1966). Following a general discussion of the order, the suborders are given separate consideration.

II. MATERIALS AND METHODS

Nearly all material used in the preparation of this work is in the British Museum (Natural History) and those specimens are referred to by the prefix B.M.N.H. A few specimens were borrowed from the Royal Scottish Museum, Edinburgh, and are prefixed by R.S.M. The prefix M.H.N.P. denotes specimens in the Muséum National d'Histoire Naturelle, Paris.

My thanks are due to Professor T. Abe of Tokyo University for the donation of three specimens of *Pterothrissus gissu*, one specimen of *Elops hawaiensis* and one of *Megalops cyprinoides*.

Techniques used in the preparation of fossil and Recent material were those used by Goody (1969b). The clearing of specimens prior to staining with ' alizarin S ' was done using the enzyme-clearing technique described by Taylor (1967).

The standard length (S.L.) of the specimens is taken from the tip of the snout to the anterior margin of the first ural centrum, unless otherwise stated. The frequent displacement of the hypurals in fossil material prevented the use of the more usual limits of this co-ordinate. The length of the head is interpreted as the distance between the tip of the snout and the posterior margin of the operculum. Linear dimensions are expressed in millimetres. Vertebral counts given are exclusive of ural centra and centra incorporated as a functional part of the neurocranium. Lastly, the first caudal vertebra is taken to be that centrum which bears a complete haemal arch and spine.

III. SYSTEMATIC DESCRIPTIONS

Cohort *TAENIOPAEDIA* Greenwood *et al.* (1967)

Superorder ELOPOMORPHA Greenwood *et al.* (1966)

Order ELOPIFORMES Greenwood *et al.* (1966)

Diagnosis. Elopomorph fishes of fusiform shape ; body rounded or compressed, never excessively deepened or elongated. Dorsal and anal fins emarginate, always distinct from the forked caudal fin. Pectoral fins held horizontally, low down on the body ; pelvic fins abdominal. Epaxial trunk musculature never extending onto the cranial roof. Dermethmoid large, overlying a cartilaginous ethmoid. Parietals meeting in the mid-line. Post-temporal fossa with a roof ; subtemporal fossa deep ; pars jugularis long ; jugular vein, hyomandibular branch of VII and orbital artery with separate openings on the lateral face of the prootic. Orbitosphenoid and basisphenoid well developed. Anterior myodome absent. Parasphenoid extending to, or near the posterior limit of the neurocranium, with teeth beneath the orbit ; basipterygoid process absent. Otophysic connection, if developed, never with an intimate connection with the ear. Palatine formed by distinct autopalatine (when ossified) and dermopalatine. Circumorbital series with supraorbital, antorbital and six infraorbitals. Rostral ossicles developed. Functional part of the upper jaw formed by the premaxilla and maxilla ; supramaxillae present but not capable of independent movement. Mandible with a fossa on the inner surface receiving the A_w division of the adductor mandibulae ; retroarticular absent. Gill arches with separately ossified dermal tooth plates and endochondral supports. First suprapharyngobranchial ossified, second suprapharyngobranchial, if present, cartilaginous. Urohyal shallow. Opercular series complete. Pectoral girdle attached to the neurocranium ; mesocoracoid arch, two or three postcleithra and a pectoral splint present. Pelvic splint present. Vertebral column with autogenous neural arches, haemal arches and parapophyses. Epineural and epipleural intermuscular bones present. Supraneurals forming a complete series between the occiput and the dorsal fin. Caudal skeleton with two free ural centra, the first supporting two autogenous hypurals, the second supporting four or five upper hypurals. Uroneurals free from centra. Nineteen principal caudal fin-rays, 17 of which are branched. Scales cycloid, overlapping and marked anteriorly by prominent radii producing a scalloped margin. Bone cells present within the anterior and lateral fields of the scales. Enlarged axillary scales present.

Suborder ELOPOIDEI Jordan, 1923

Diagnosis. Elopiform fishes in which the cranium is never broad. Sensory canals of the head largely enclosed by bone; supraorbital sensory canal running through parietal; ethmoid commissure complete, running through dermethmoid. Post-temporal fossae large, directed anteriorly; sub-epiotic fossae absent. Intercalar large, extending anteriorly to contact the prootic, forming a prootic-intercalar bridge. First vertebral centrum articulating with facets upon the exoccipitals and basioccipital and forming a functional part of the neurocranium. Lateral ethmoid not in contact with the parasphenoid; parasphenoid narrow. Hyomandibular-metapterygoid cup developed. Premaxilla small, never associated with a sensory canal. Two supramaxillae. Articular (angular) and endosteal articular (articular) separate ossifications. Dentition of small villiform teeth on the dermal jaws, vomer, parasphenoid, dermopalatine, endopterygoid, ectopterygoid and basibranchial and basihyal dermal plates. Gular plate large, always horizontal. Gill-rakers prominent upon the first three gill arches. Supratemporal large, meeting its partner in the dorsal mid-line. Caudal fin with seven hypurals; the bases of the inner fin-rays expanded. Scales with concentric circuli in the anterior and lateral fields.

Family **ELOPIDAE** Bonaparte, 1846

Diagnosis (emended). Elopoid fishes in which the body is rounded. Cranium shallow with the mouth terminal. Neurocranium in which the roof is flat; the parietals retain evidence of middle pit-lines; the autosphenotic spine and the epiotic process are weakly developed; the post-temporal fossae extend forward to the level of the autosphenotics and remain separate from one another; the dilatator fossa is roofed. Otophysic connection absent. Two rostral ossicles present (only known in *Elops*). Quadrate/mandibular articulation at or behind the level of the posterior orbital margin. Maxilla shallow, extending posteriorly beyond the level of the eye. Mandible shallow with a weakly developed coronoid process situated posteriorly. Pseudobranchiae present in Recent genus. Dorsal and anal fins short based. Pelvic fins originating beneath or behind the dorsal fin. First anal pterygiophore short. Urodermal present. Scales with at least six anterior radii, otherwise marked only by fine circuli. Lateral line tubes unbranched.

Genus ***ELOPS*** Linnaeus, 1766

Diagnosis (emended). Elopid fish in which the cranial bones are devoid of ornamentation. Dermethmoid without ventro-lateral projections. Circumorbital series with a large first infraorbital which meets the supraorbital and so excludes the antorbital from the orbital margin; infraorbital canal without bone-enclosed branches. Union of infraorbital, antorbital and ethmoid commissure sensory canals lying within skin. Supramaxillae narrow, posterior member without strengthening ridge. Quadrate with anterior and posterior margins of equal length. Ceratohyal imperforate. Preoperculum with a slight posterior expansion, the contained sensory canal running at the anterior margin of the bone and opening to the surface by numerous pores. Vertebral count high, averaging 75. Caudal fin without fringing fulcra.

TYPE-SPECIES. *Elops saurus* Linnaeus, 1766.

REMARKS. Although many references have been made to *Elops* in discussions of teleostean phylogeny, no complete osteological description exists. The direct relevance of such a study to a work of this nature justifies the inclusion of a description here. *Elops hawaiensis* Regan has been chosen as the species to be described since the size range of available individuals allows an evaluation of ontogenetic changes.

Regan (1909) recognized seven species of *Elops*; *E. saurus* Linnaeus from the east coast of Middle America and *E. affinis* Regan from the west coast, *E. senegalensis* Regan and *E. lacerta* Cuvier & Valenciennes from the west coast of Africa, *E. machnata* Forskål, *E. hawaiensis* Regan and *E. australis* Regan from the Indo-Pacific. The differences between these species are primarily differences in gill-raker, vertebral and scale counts. Whitehead (1962) did not consider *E. australis* a valid species and placed it in synonymy with *E. hawaiensis*. *E. machnata* is also very much like *E. hawaiensis*, differing only in vertebral counts (63–64 in the former against 66–69 in the latter) and by the fact that when the mouth is closed the premaxillary tooth band is exposed in *E. hawaiensis* but is covered by the lower jaw in *E. machnata* (Regan 1909; Whitehead 1962). Both of these differences appear to be trivial. The former is particularly unsatisfactory while specimens of both Indo-Pacific species show variable conditions of the ‘ exposed ’ or ‘ covered ’ state. It is likely that only one Indo-Pacific morphospecies exists.

The differences between *E. hawaiensis* and the type-species are slight and have been illustrated by Whitehead (1962). Certain portions of the osteology of *Elops* have been satisfactorily described in recent literature and where this has been done the relevant references are cited without further comment.

Elops hawaiensis Regan, 1909

(Text-figs. 1–11)

1909 *Elops hawaiensis* Regan: 37.

DIAGNOSIS. See Regan (*op. cit.*).

HABITAT. Coastal waters of the Indo-Pacific.

DESCRIPTION. *Neurocranium.* The neurocranium is three times as long as deep. The maximum width of the cranium occurs at the occiput and is equal to one and a half times the depth of the neurocranium. The cranial cavity occupies about one-third of the total neurocranial length.

Much of the cranial roof is formed by the paired frontals. Each frontal is narrow anteriorly but widens at the level of the lateral ethmoid and again above the autosphenotic spine. Above the orbit the lateral margins of the frontals are parallel, a resemblance to leptolepids rather than pholidophorids. Posteriorly each frontal ends squarely, with a slight overlap above the parietal and pterotic of its side. The mutual interfrontal suture is straight in young individuals, where there may be a divergence of the bones anteriorly exposing the ethmoid cartilage. In the adult, however, the frontals meet one another throughout their length and the suture line becomes wavy posteriorly. Ornamentation upon the frontal is confined to the ridges associated with the sensory canals and is described below.

The anterior end of the cranial roof is formed by the median dermethmoid (rostral of Gardiner 1963 and Nybelin 1956, 1967a). The dermethmoid is long, unlike that bone in pholidophorids and Liassic leptolepids, and overlaps the frontals, a fact which reinforces its interpretation as a dermal element. The ethmoid commissure runs transversely across the dermethmoid at the level of the maximum width of the latter element. The commissure, which is relatively large in young individuals, is contained within a bony tube perforated dorsally by two pores. In young individuals this bony tube appears to be an ossification distinct from the underlying dermethmoid but in older individuals it appears as an integral part of that bone.

The nasals, although not strictly part of the neurocranium, may be considered here as they are closely associated with the roofing bones. Each nasal is tube-like, barely larger than the sensory canal that it carries. The nasal is pierced dorsally by four large pores. Gosline (1965) reported the presence of a small prenasal ossicle in *Elops saurus*, which according to Nybelin (1967a) may become incorporated in the lateral rostral ossicle. I have found no such prenasal in *E. hawaiensis*. However, the possibility of there being a prenasal ossicle in some species of *Elops* is interesting since it may be indicative of a trend among elopiform teleosts, that is, a general tendency toward fragmentation of the dermal bones of the snout.

The parietal is rectangular and meets its partner in the mid-line except posteriorly where the supraoccipital intervenes for a very short distance. There are recognizable differences in the dimensions of the exposed part of the parietal between young and old individuals. In the young the length of each parietal exceeds its width whereas in the adult the converse is true. The change in shape is due to two factors: differential growth of the parietal in which lateral growth proceeds at a greater rate than longitudinal growth, and secondly the frontals overlap the parietals to a greater extent in older fish. Ornamentation upon the parietals, like that of other cranial bones, is restricted to ridges associated with the sensory canals.

The postero-lateral region of the neurocranial roof is formed by the dermal portion of the pterotic. The dermal portion of the pterotic forms much of the roof of the post-temporal fossa. The lateral and posterior faces of the pterotic are formed by the thicker but less dense endochondral bone. As is usual among teleosts there is no clear demarcation between the dermal and endochondral portions of the pterotic (Gosline 1969 reports the presence of separate autopterotic and dermopterotic in *Alepocephalus*). The lateral face of the pterotic forms the posterior region of the dilatator fossa, much of the hyomandibular facet and the roof of the deep

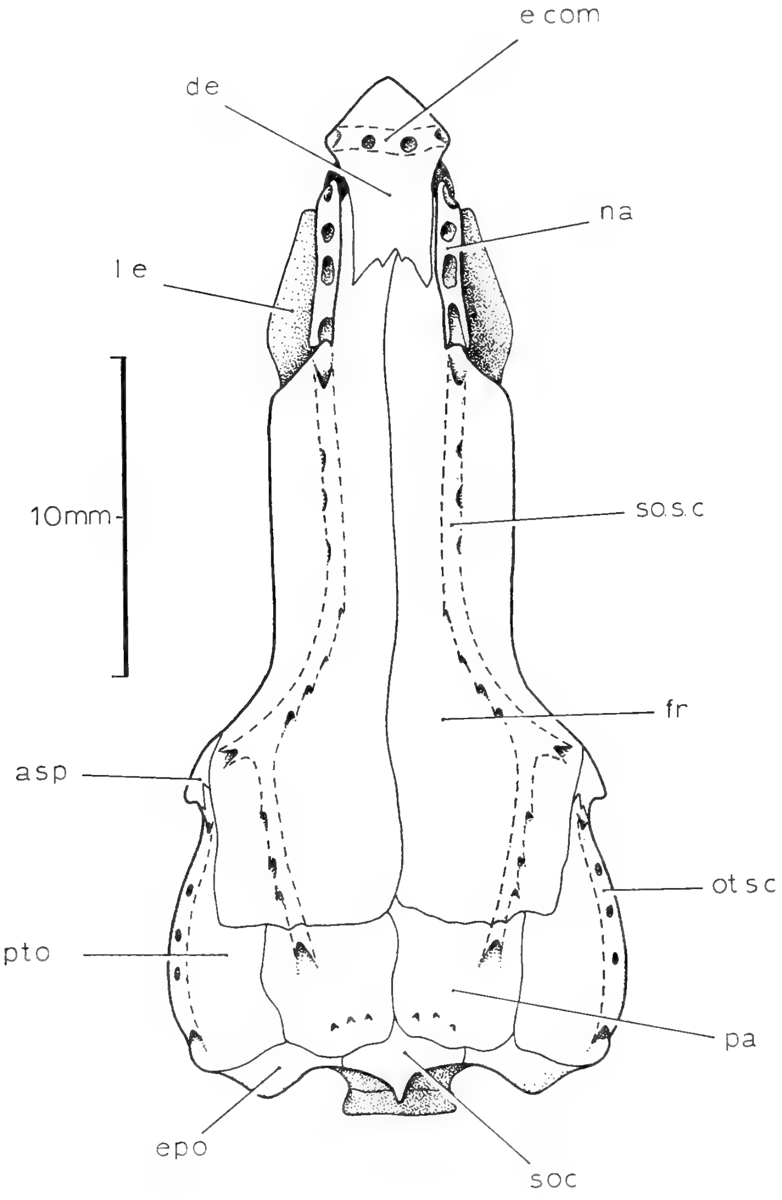

FIG. 1. *Elops hawaiensis* Regan. Neurocranium in dorsal view; this and Text-figs. 2–5 are based on a specimen of 208 mm S.L.

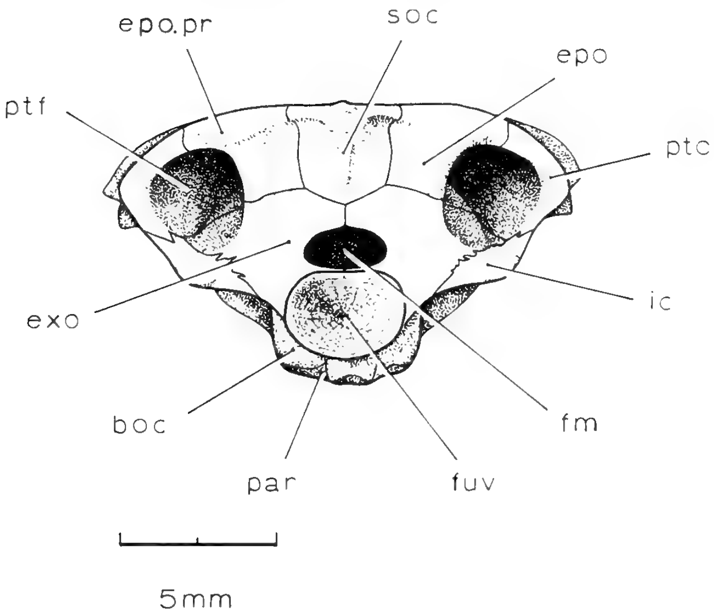

Fig. 2. *Elops hawaiensis* Regan. Neurocranium in posterior view.

subtemporal fossa. A swelling forming an arc above the subtemporal fossa and beneath the hyomandibular facet indicates the path taken by the horizontal semicircular canal through the pterotic. Anteriorly and posteriorly the semicircular canal descends through the prootic and exoccipital respectively before entering the cranial cavity. Medially the pterotic forms the lateral wall of the post-temporal fossa. The posterior face of the pterotic contacts the epiotic above and the exoccipital below the opening of the post-temporal fossa. The union of the pterotic and exoccipital may only be seen in posterior view if the cap-like intercalar is removed.

The epiotic is seen in dorsal and posterior views of the neurocranium. From the former aspect it is represented by a knob-like process, protruding posteriorly from beneath the parietal and pterotic. In posterior view the epiotic forms part of the dorsal and medial margin of the opening leading to the post-temporal fossa.

Between the epiotics lies the supraoccipital which, in posterior view, is pentagonal. The flat surface of the supraoccipital is interrupted only by a weakly defined vertical crest which becomes more prominent dorsally. In dorsal view the supraoccipital is seen as a small triangle, the apex of which lies between the posterior ends of the parietals. Beneath the roof the supraoccipital extends forward as a median and two antero-lateral projections. The latter reach forward to meet the frontal of either side and in so doing form the median walls of the post-temporal fossae. The supraoccipital is pierced by canals which carry the posterior vertical semicircular canal of either side. Laterally, this semicircular canal descends through the epiotic where its passage is visible externally as a ridge along the medial margin of the post-temporal fossa opening. Ventrally, the posterior vertical semicircular canal runs through the exoccipital before opening to the endocranial cavity immediately above the vagus foramen. Ridewood (1904: 39) noted that in *Elops saurus* the internal limit of the deep subtemporal fossa is formed by the supraoccipital. The supraoccipital of *E. hawaiensis* is not as extensive as that in the type-species and does not play any part in the subtemporal fossa.

The exoccipital exhibits both a lateral and posterior face. The latter face contacts the epiotic and supraoccipital above, the basioccipital below, and with its fellow of the opposite side surrounds the foramen magnum. In young individuals the margin of the foramen magnum is often incomplete ventrally. In its dorsal extent the lateral face of the exoccipital is turned sharply inwards to form the posterior wall of the subtemporal fossa, while ventrally the exoccipital is inflated and together with the prootic and basioccipital forms the outer wall of the saccular recess. The saccular recess and the contained otolith are relatively larger in younger individuals. Three, occasionally four, foramina pierce the lateral face of the exoccipital. Posteriorly there is a large vagus foramen directed ventro-laterally and slightly posteriorly. Anteriorly, close to the exoccipital-prootic suture, there is an antero-ventrally directed glossopharyngeal foramen. The third constantly occurring foramen is situated immediately in front of the vagal foramen and marks the point at which a small branch of the glossopharyngeal nerve left the cranial cavity. This accessory glossopharyngeal foramen is, in some specimens, preceded by another very small foramen whose function could not be determined; it may have carried a small blood vessel.

The intercalar ossifies very early in the development of the neurocranium. The main body of the intercalar forms a cap over the triradiate union of exoccipital, epiotic and pterotic. The ventral limb of the post-temporal is attached to this main body. In lateral view the intercalar is produced ventrally and anteriorly. The ventral extension partially surrounds the vagus foramen while the well-developed anterior extension reaches forward to interdigitate with a posterior outgrowth of the prootic. Together the prootic and intercalar form a bridge which stands clear of the neurocranial wall, leaving a small foramen which may be seen in ventral view (cf. *Leptolepis dubia* figured by Patterson 1967a: fig. 5). A small branch of the glossopharyngeal nerve passes up through this foramen but it is doubtful if this is the primary function of the foramen since it is inordinately large for the nerve which passes through.

The basioccipital is 'W'-shaped in cross section, the lateral wings of the 'W' enclosing the saccular recess of either side while the space beneath the central arms represents the posterior myodome. The posterior portion of the basioccipital meets the paired exoccipitals above in a triradiate suture, and this posterior face articulates with a thin vertebral centrum. This first centrum is firmly united with the cranium, so much so that in older individuals it is difficult to recognize as a discrete entity. Ventrally this centrum bears parapophyses but no pleural ribs, while dorsally there is an autogenous neural arch and spine. In small specimens the centrum is still pierced by a notochordal foramen. The occipital condyle of lower teleosts is primitively formed by the inclusion of a centrum into the neurocranium, but rarely is there any associated neural arch. Thus *Elops* would appear to represent a primitive

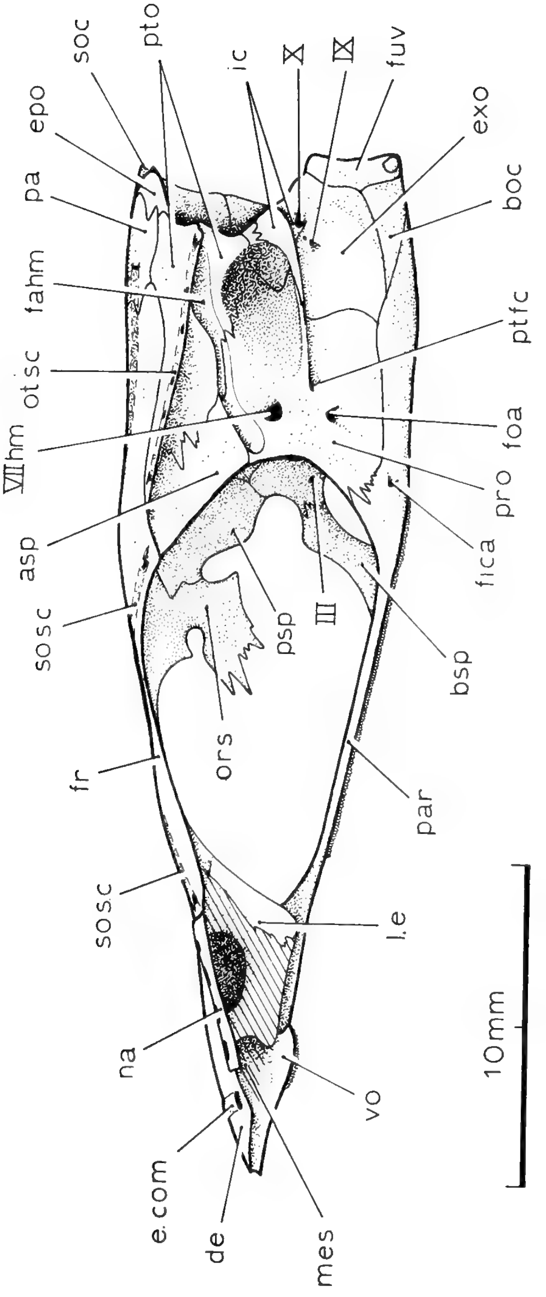

FIG. 3. *Elops hawaiensis* Regan. Neurocranium in left lateral view. Hatched areas represent cartilage.

stage, directly comparable to *Tarpon* but more advanced than that described for *Heterotis* where according to Greenwood (1968) there is also a pleural rib and epicentral bones associated with this centrum. It is generally assumed that the neural arches associated with this centrum are lost in most teleosts but the situation may be more complex since Gosline (1969) records that in *Alepocephalus* the neural arches have become detached from the centrum and are incorporated into the neurocranium. Clearly the occipital condyle region of the teleost neurocranium warrants closer attention.

The prootic is the largest endochondral component of the neurocranium and, as is usual in teleosts, is complicated in shape. The prootic is disposed in a vertical and horizontal plane, the former consisting of transverse and longitudinal faces. The horizontal part of the prootic extends medially from the lateral face beneath the level of the pars jugularis and meets its fellow in the mid-line, so forming the prootic bridge. The anterior margin of the prootic bridge is deeply indented in the mid-line, forming the posterior margin of the pituitary foramen. The anterior border of this foramen is formed by the basisphenoid. Posteriorly the prootic bridge is sutured with the basioccipital so separating the cranial cavity above from the posterior myodome below. The abducens nerve pierces the prootic bridge near to its junction with the lateral vertical face of the prootic.

The lateral vertical face of the prootic is depressed postero-dorsally where it forms the anterior region of the subtemporal fossa. Postero-ventrally the prootic is inflated to form part of the wall of the otolith chamber. Within the lateral face of the prootic runs the long pars jugularis. Posteriorly the pars jugularis opens to the lateral face of the neurocranium by the jugular foramen, close to the prootic-exoccipital suture. Immediately above the jugular foramen the prootic is raised into a short spine which extends posteriorly and interdigitates with an anterior limb of the intercalar. The hyomandibular foramen opens to the surface of the prootic above the level of the pars jugularis to which it is connected by a short canal. Above the foramen the path taken by the hyomandibular ramus is seen as a faint groove. From the floor of the pars jugularis a short canal passes ventrally through the prootic and splits into two branches, one opening on the medial face, the other on the lateral face. The former carries the palatine branch of the facial, the latter carries the orbital artery.

The medial wall of the pars jugularis is perforated by a single large foramen through which pass the roots of the trigeminal, facial and profundus ciliaris nerves. The pars ganglionaris is simply represented by a small depression on the medial aspect of the prootic. The gasserian and geniculate ganglia are lodged within this depression.

The anterior, transversely orientated face of the prootic is small. It meets the autosphenotic and pterosphenoid dorsally, the basisphenoid ventro-medially and the parasphenoid ventro-laterally. Medial to the large anterior opening of the pars jugularis there is a smaller oculomotor foramen.

The autosphenotic is tetrahedral, the apex of the tetrahedron being produced laterally as a small spine to which the levator arcus palatini musculature is attached. Laterally the autosphenotic forms the anterior part of both the dilatator fossa and the

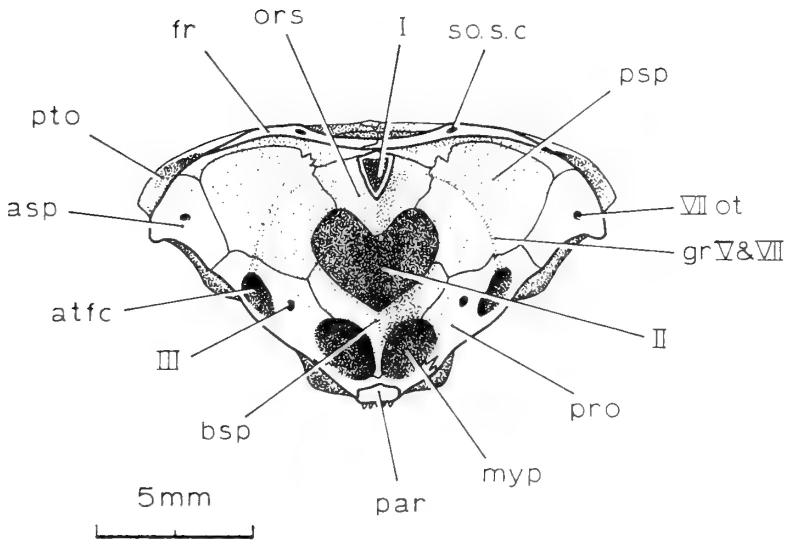

FIG. 4. *Elops hawaiensis* Regan. Neurocranium in orbital view.

hyomandibular facet. The orbital face of the autosphenotic contacts the prootic, pterosphenoid and frontal and is pierced by a foramen conveying the otic branch of the facial to innervate the otic sensory canal. Internally the autosphenotic forms the anterior wall of the post-temporal fossa. Ridewood (1904) stated that in *Elops saurus* the anterior limit of the post-temporal fossa is formed by the pterosphenoid (alisphenoid). This is not the case in *E. hawaiensis.*

The lateral margins of the heart-shaped optic foramen are formed by the pterosphenoid of either side which lies medial to both the prootic and autosphenotic. The surface of the pterosphenoid is marked by a groove which curves upwards and forwards from the opening to the pars jugularis. This groove contains the superficial ophthalmic branches of V and VII. The trochlear nerve passes out of the cranial cavity through the optic foramen.

The orbitosphenoid lies anterior to the pterosphenoids. The anterior margin of the orbitosphenoid is perforated by a large foramen through which pass the olfactory tracts. Ventrally the orbitosphenoid is produced as a membranous interorbital septum. Posteriorly the orbitosphenoid forms the dorsal margin of the optic foramen. The ventral margin of the optic foramen is formed by the ‘ wings ’ of the ‘ Y ’-shaped basisphenoid which contact the prootic and pterosphenoid of either side. The laterally flattened stem of the basisphenoid passes antero-ventrally to meet the parasphenoid so dividing the entrance to the posterior myodome. The basisphenoid stem ossifies late in ontogeny.

The parasphenoid is long, extending from its contact with the vomer anteriorly to the hind edge of the basioccipital. Beneath the orbit the parasphenoid is relatively narrow but beneath the otic region it is broader as it forms the floor of the posterior

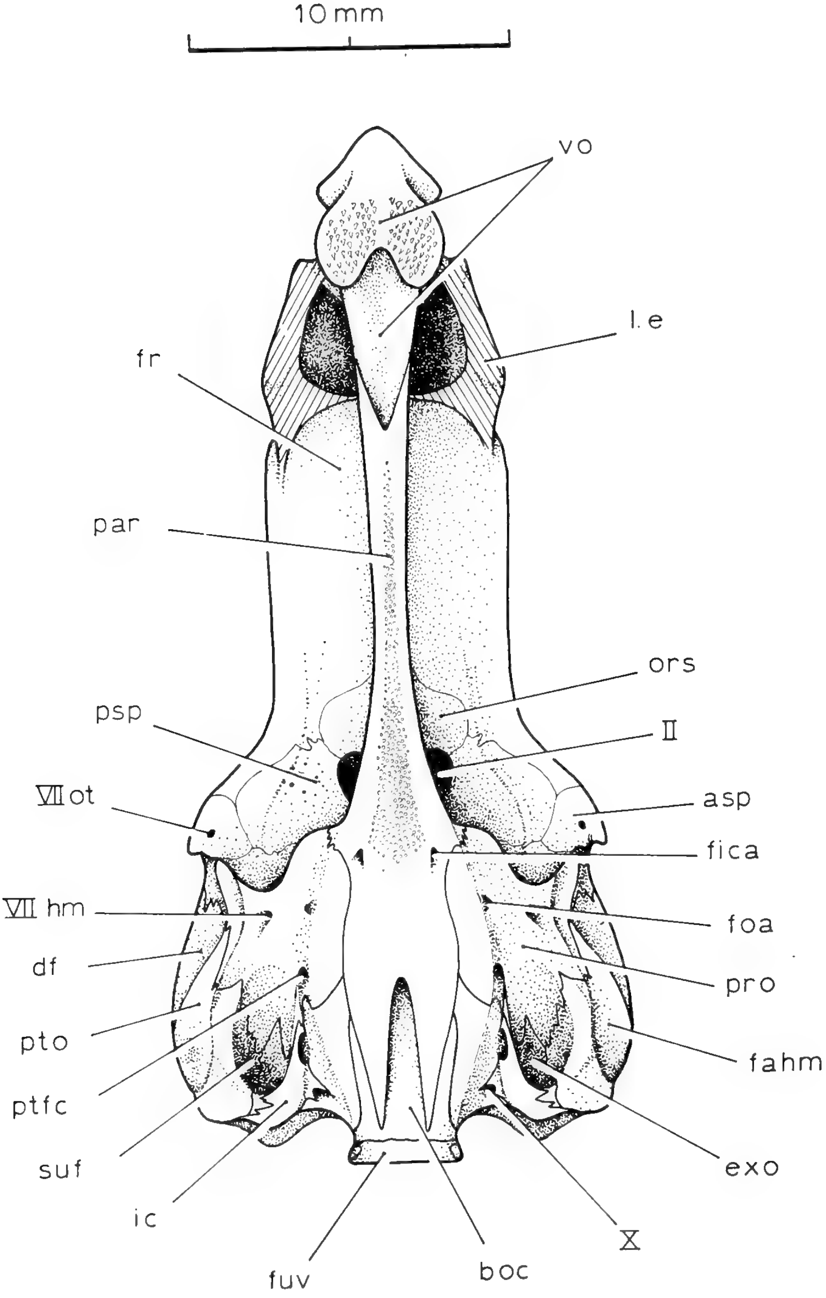

FIG. 5. *Elops hawaiensis* Regan. Neurocranium in ventral view. Hatched areas represent cartilage.

myodome. The parasphenoid is produced dorsally as a shallow ascending wing which partially overlaps the prootic. A foramen for the internal carotid artery occurs within the parasphenoid at the base of the ascending wing. Posteriorly the parasphenoid ends in a notch forming the lower edge of a foramen leading to the myodome, the dorsal edge of this foramen being formed by the basioccipital. Beneath the orbit the parasphenoid bears teeth. In young individuals the teeth are very small and clustered along the margins of the bone but in adults the pattern changes to a dense and complete covering of small villiform teeth. The parasphenoid is usually pierced in the mid-line beneath the basisphenoid by a foramen for the bucco-hypophysial canal but in the specimen figured here (Text-fig. 5) it is closed ventrally.

The vomer consists of a broad head and a spear-shaped shaft which extends posteriorly beneath the lateral ethmoid. The paired vomerine tooth plates are raised upon short pedicels. In small individuals each toothed area is separated from its partner and bears about 20 small recurved teeth. During growth the number of teeth increases to about 60 and the toothed areas of either side approximate to one another in the mid-line. Even in the largest specimens examined the toothed area retains its identity as a paired element.

Much of the snout region is formed by cartilage. Between the dermethmoid above and the vomer below the ethmoid cartilage separates the nasal capsules of either side. The posterior, ventral and anterior walls of the nasal capsule are composed of ethmoid cartilage. Beneath the anterior region of the solum nasi the cartilage is somewhat denser than elsewhere and forms an oval facet for the articulation of the palatine head. Two facets for jaw articulation occur upon the lateral face of the cartilage above the vomer. The posterior of these receives the head of the maxilla while the anterior receives the premaxilla. In the largest individuals the extreme anterior tip of the ethmoid cartilage may show a limited amount of endochondral ossification. Posteriorly the lateral edge of the planum antorbitale ossifies perichondrally to form the lateral ethmoid. The olfactory tract and the nasal branch of the orbitonasal artery pierce the planum antorbitale through a large foramen olfactorium advehens. There is no anterior myodome.

Hyopalatine bones. The hyomandibular is a stout element with a single broad articulatory head (a distinction from the type-species which shows a weakly divided head, Ridewood 1904) which is inclined antero-ventrally. The hyomandibular is produced postero-ventrally as a narrow shaft. Dorsally the posterior margin of the hyomandibular projects as a prominent opercular process which articulates with a cup-shaped depression on the operculum. The hyomandibular ramus of VII and the efferent hyoidean artery pierce the hyomandibular immediately beneath the anterior limit of the head and run obliquely through the bone to emerge beneath the opercular process before running down in a groove on the posterior edge of the shaft. Anteriorly the head of the hyomandibular is produced as a thin wing of bone which lies medial to the dorsal part of the metapterygoid. The cup-shaped space left between the hyomandibular and metapterygoid, the hyomandibular-metapterygoid cup, receives deeper fibres of the levator arcus palatini.

The metapterygoid is irregular in shape. Its dorsal margin is turned horizontally, medial to that part referred to above which overlaps the hyomandibular. The anterior border of the metapterygoid overlaps the endopterygoid, while the ventral margin is in synchondral union with the quadrate.

The quadrate bears a stout articulatory condyle which in adult fish lies vertically beneath the head of the hyomandibular. The posterior margin of the quadrate is thickened. Upon the medial surface of the quadrate a deep groove runs close to the posterior margin and accommodates the ventral end of the styliform symplectic. The dorsal end of the latter is united with the hyomandibular shaft by cartilage.

The ectopterygoid is composed of two limbs, the posterior grooved to fit the anterior margin of the quadrate and the longer anterior limb disposed more horizontally. The dorsal edge of the ectopterygoid is thickened and to this thickening is attached a tough fold of skin which inserts on the medial face of the overlying infraorbitals. Gosline (1965) pointed out that there was no ectopterygoid process in *Elops* but the thickened ridge in *E. hawaiensis* may be considered as such a rudimentary process. The oral surface of the ectopterygoid bears many small villiform teeth.

The convex oral surface of the endopterygoid is covered with many small villiform teeth, continuous with those upon the ectopterygoid.

There is a small dermal palatine (dermopalatine) but no ossified autopalatine. The palatine cartilage overlaps the anterior ends of the ectopterygoid and endopterygoid posteriorly. Anteriorly the cartilage is slightly swollen and bears a facet upon the dorso-medial surface which fits against the floor of the nasal capsule. The ventro-lateral surface of the palatine cartilage articulates with the maxilla but there is no special facet developed. The dermopalatine is represented by a tooth plate. The teeth borne by this plate are continuous with those on the ectopterygoid and endopterygoid but are more like those of the vomer in shape, being pointed and recurved.

Dermal upper jaw. The upper jaw extends from the tip of the snout to behind the orbit. The relative length of the upper jaw increases slightly throughout life. The premaxilla forms a little less than one-third of the convex oral margin. The premaxilla is relatively shallow, the maximum depth being equal to less than one-quarter of its length and situated towards the anterior end. From its point of maximum depth the bone tapers in both directions. The oral surface of the premaxilla bears a band of small teeth. Each tooth is conical and bears a pointed enamel cap, set at an angle to the main axis of the tooth. Basally the tooth is set within a shallow socket.

The maxilla is elongate and deepest posteriorly. Anteriorly the maxilla curves both dorsally and medially to end in a simple rounded head which articulates directly with the ethmoid. Behind the maxillary head the dorsal surface of the maxilla bears a palatine process which articulates with the ventro-lateral aspect of the palatine through a biconcave sliver of cartilage. The oral margin of the maxilla bears a band of small teeth similar to those upon the premaxilla. Posteriorly the tooth band extends on to the lateral surface of the bone.

There are two supramaxillae. The anterior supramaxilla is produced anteriorly as a spine. The posterior bone also bears an anterior spine which overlies part of the anterior supramaxilla. Both supramaxillae are without strengthening ridges and are relatively immobile, unlike these bones in clupeoids.

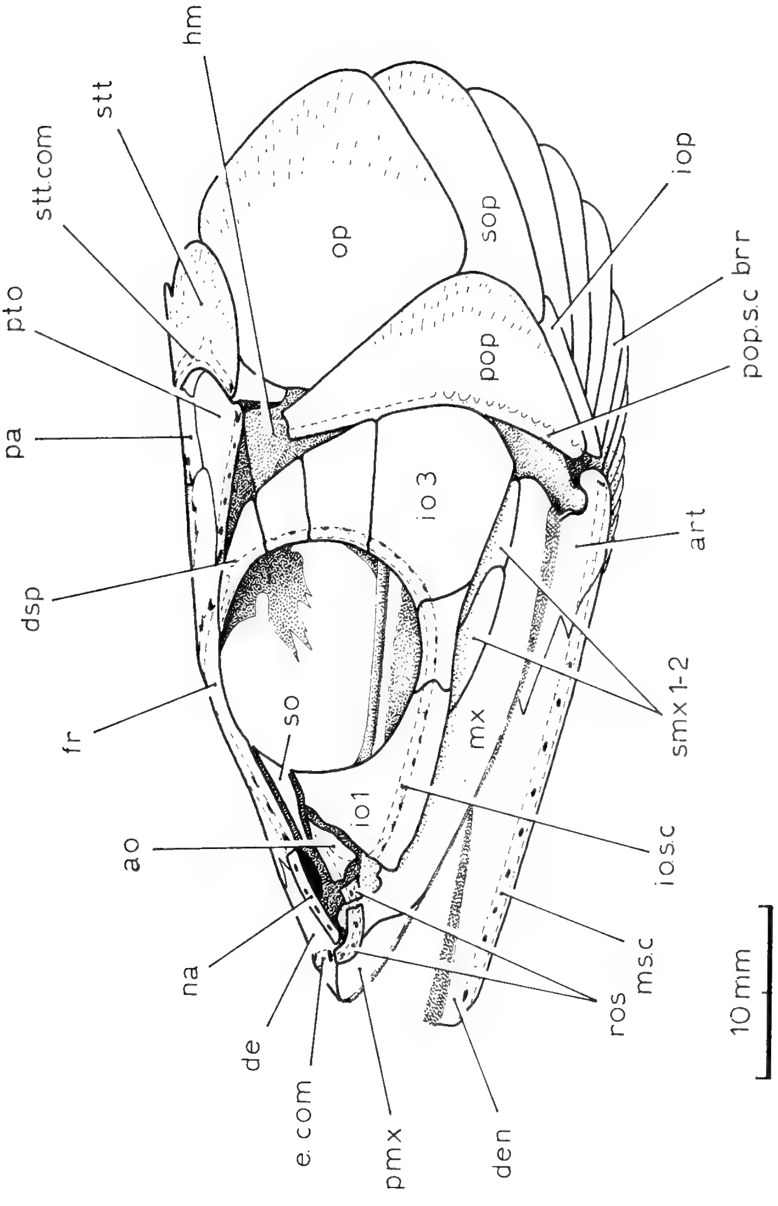

FIG. 6. *Elops hawaiensis* Regan. Cranium in left lateral view. Composite of several specimens.

Mandible. Little may usefully be added to what Ridewood (1904) has described in *Elops saurus.* Mention may be made of the deep fossa on the medial surface of the dentary which receives the A_w division of the adductor mandibulae. This fossa is relatively deep in *Elops*, its development probably being advanced and perhaps correlated with the predatory habits of this genus since it is absent in the microphagous clupeoids.

Circumorbital series. The circumorbital ring is incomplete dorsally. The supraorbital is the only anamestic component of the series. It is a narrow bone which lies close against the frontal. The ventral end of the supraorbital is overlain by the antorbital. This latter bone and the snout ossicles have been described and figured by Nybelin (1956, 1967a) in *Elops saurus* and the situation is the same in *E. hawaiensis.*

The first infraorbital is very deep anteriorly but shallow posteriorly. Characteristically the first infraorbital contacts the supraorbital and so excludes the antorbital from the orbit. The second infraorbital is very short and shallow and meets the expanded third infraorbital in an oblique suture. The fourth and fifth infraorbitals, like the third, are longer than deep. The sixth infraorbital, or dermosphenotic, consists of a shallow base which is produced antero-dorsally as a process which lies tightly against the frontal.

Hyoid arch, gill arches and gular plate. These structures and associated dermal elements have been dealt with in various papers; the hyoid and gill arches by Ridewood (1904) and especially Nelson (1968a,b, *E. hawaiensis*, and 1969a), the dentition of the mouth cavity by Nybelin (1968) and the gular plate by Jessen (1968). Although the above authors described *Elops saurus* there is little difference in *E. hawaiensis.*

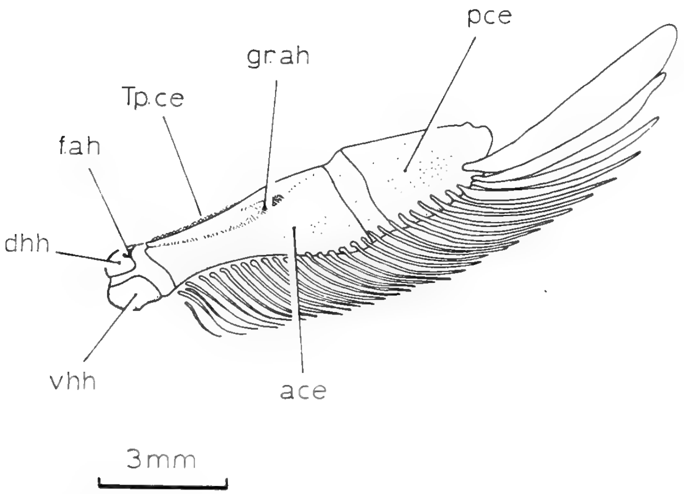

FIG. 7. *Elops hawaiensis* Regan. Hyoid bar and branchiostegal rays in left lateral view; this and Text-figs. 8–11 based on an alizarin preparation of B.M.N.H. 1962.4.3.1, 62 mm S.L.

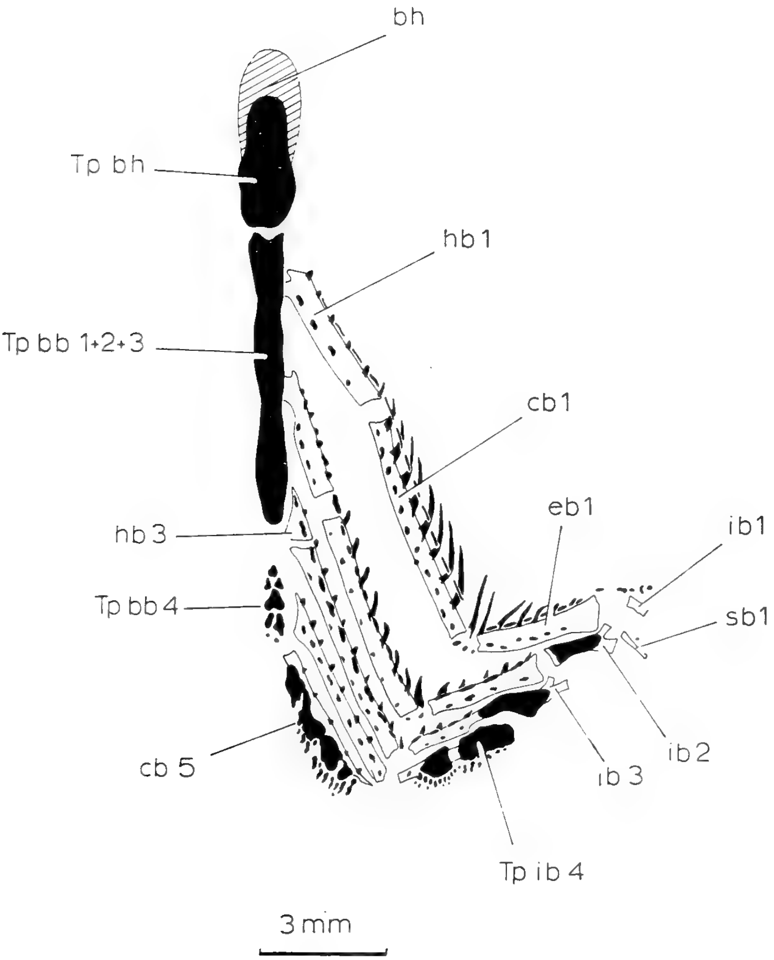

FIG. 8. *Elops hawaiensis* Regan. Gill arches of right side in dorsal view. The dorsal elements have been turned back exposing their ventral aspect; the second suprapharyngobranchial is obscured by ib3, and the fourth infrapharyngobranchial is covered by Tpib4. Hatched area represents cartilage, black represents tooth plates and gill-rakers.

The only additional feature worthy of note is the attachment of the gill arches to the neurocranium, an attachment which is effected through the first infrapharyngobranchial and suprapharyngobranchial. The former element is attached through a small disc of cartilage to the parasphenoid behind the internal carotid foramen in that bone. A posterior attachment to the neurocranium is effected by a ligament which passes from the dorsal limb of the first epibranchial to the anterior extension of the intercalar. Within this ligament the first suprapharyngobranchial is represented as a small ossified rod situated just above the first epibranchial.

Cephalic sensory canal system. The main canals run within bony tubes which are perforated by pores. The sensory canals produce ridges upon the bones through which they run. The junctions between the major canals lie in the skin.

The lateral line passes on to the cranial roof by a pore at the postero-lateral corner of the pterotic. The otic canal runs through the extreme lateral edge of the roofing portion of the pterotic and opens anteriorly above the autosphenotic spine. The dorsal surface of the otic canal is perforated by three or four pores. The posterior opening of the otic canal lies adjacent to a pore in the supratemporal and also adjacent to but at a distance from the top of the preopercular canal. The triradiate union between the supratemporal commissure, otic and preopercular canals occurs within the skin.

The anterior opening of the otic canal lies adjacent to two pores ; one within the frontal which is the lateral opening of the supraorbital canal and one from the dorsal surface of the dermosphenotic which represents the dorsal limit of the infraorbital canal. Again, the union of these canals lies in the skin.

From its union with the otic and infraorbital canals, the supraorbital canal curves medially and then anteriorly to run the length of the frontal. A large branch of the supraorbital canal is given off posteriorly and this runs back on to the parietal where it opens to the surface by a single terminal pore, behind which there is in some specimens a continuing shallow groove. The groove is interpreted as representing the anterior pit-line. The parietal is also marked by three small pores arranged in a transverse row. Such a pore arrangement is similar to the middle pit-line of halecostomes and leptolepids. In these latter fishes the pores are set in a shallow groove but no such connecting groove exists in *Elops.* The main supraorbital sensory canal opens to the surface by several pores on both the lateral and medial aspects of the canal. Above the epiphyseal region there is a predominance of medial pores, while above the orbit and otic regions lateral pores are more common.

The infraorbital canal runs very close to the orbital margin of the infraorbitals, opening to the surface by a series of posterior and inferior pores. The neuromast distribution has been noted by Nelson (1969b). Anteriorly the infraorbital canal joins with the antorbital branch and the ethmoid commissure. The distribution of the sensory canals in this region has been described by Nybelin for *Elops lacerta* (1956, 1967a) which in all respects is similar to *E. hawaiensis.*

The preopercular canal runs at the anterior margin of that bone and in its ventral half opens to the surface by ten to fifteen pores. Ventrally the preopercular canal is continuous with the mandibular canal which is contained within the articular and dentary. The mandibular canal opens to the surface by a series of large pores.

Opercular series. The opercular bones of *Elops saurus* have been described by Ridewood (1904). In most respects they are similar to those of *E. hawaiensis,* differing only in proportions. Further description is unnecessary.

Pectoral girdle and fin. The supratemporal, although not strictly part of the shoulder girdle, may be considered here. As in all elopoids the supratemporal is very large and thin, fully justifying its alternative name of the ' scale bone '. The supratemporal has a straight anterior margin which extends from the postero-lateral corner of the pterotic to the mid-line. The posterior margin is broadly curved,

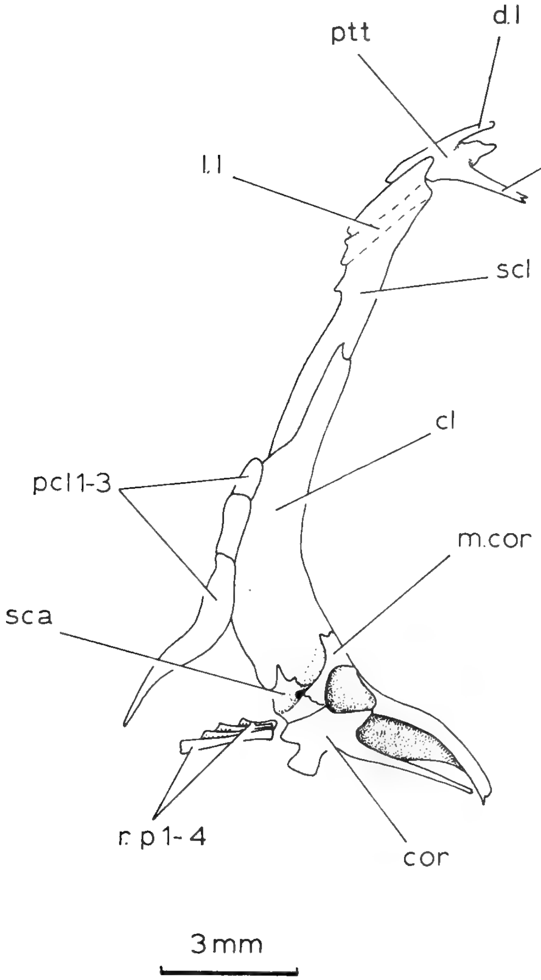

FIG. 9. *Elops hawaiensis* Regan. Pectoral girdle of the left side in medial view.

showing an indentation in the middle of its length. The growth pattern of the supratemporal refutes any suggestion that it is formed of two elements. The supratemporals of either side meet one another in the mid-line covering both the epiotics and the supraoccipital. In consequence of this median union the supratemporal commissure is completely enclosed by bone. The latter canal opens to the surface by a few posterior pores. The main lateral line pierces the ventral surface of the supratemporal.

The post-temporal is composed of a main body which bears three processes. The body of the bone is a small flat plate on the underside of which there is a small depression which receives the dorsal end of the supracleithrum. The lateral line runs through the lateral margin of the post-temporal. Two of the three processes mentioned above are merely extensions of the anterior margin of the main body. Medially there is a pointed dorsal limb which overlies the epiotic process. Laterally, there is a very small limb which reaches forwards but fails to reach the pterotic. The third process originates from the undersurface of the main body and passes antero-ventrally to become firmly anchored to the intercalar.

The supracleithrum is long, narrow and inclined postero-ventrally. The anterior margin is slightly thickened. The lateral line runs obliquely through the upper half. Ventrally the supracleithrum overlaps the cleithrum. The latter element is, as usual, the largest single component of the shoulder girdle. From a narrow dorsal portion the bone expands as it curves antero-ventrally and medially to contact its fellow in the ventral mid-line. The anterior margin of the cleithrum is turned inwards to form both the posterior wall of the gill chamber and a site of origin for the sterno-hyoideus musculature. There are three narrow postcleithra attached to the medial surface of the cleithrum.

The endochondral coracoid is attached to the ventral limb of the cleithrum. In its middle region it fails to contact the cleithrum and there is instead a large space, the interosseous foramen of Starks (1930). Posteriorly the coracoid contacts the scapula laterally and the mesocoracoid dorsally.

The scapula spreads over the inner face of the cleithrum. The scapula completely encloses the scapular foramen. Posteriorly the margin of the scapula bears a deep notch, the point of insertion of the outermost fin-ray. The mesocoracoid is represented by a thin bar of bone which passes dorsally from its union with the scapula and coracoid. The dorsal part of the mesocoracoid is expanded and like the scapula spreads over the inner face of the cleithrum.

Support of the dermal fin-rays is shared by the endochondral girdle and the radial elements. The outer ray is attached directly to the scapula. There are four ossified proximal radials which articulate with the coracoid. The longest of the proximal radials is the innermost, the shortest the outermost. A further row of cartilaginous distal radials may be recognized but neither their number (usually six to eight) nor their distribution is constant from individual to individual or even from one side of a specimen to the other. The distal radials appear to play little part in the support of the fin.

There are 15–16 branched rays plus the outer unbranched ray. The longest is the second in the series, the outermost branched ray. At the base of the first ray there is a small triangular pectoral splint bone which is positioned equally over both halves of the ray.

Pelvic girdle and fin. The pelvic fin originates beneath the anterior half of the dorsal fin. The fin-rays are supported by both radials and a pelvic bone. The latter is triangular, the apex directed anteriorly. Posteriorly the margin of the pelvic bone is covered by cartilage. Two or three cartilaginous radials articulate with the posterior margin. An ossified inner radial articulates with the postero-medial aspect of the pelvic bone. This inner radial is represented by a curved splint, the proximal end of which lies between the bases of the inner four rays.

There are 15–16 pelvic fin-rays of which the outermost is unbranched. The third ray is the longest of the series. At the base of the upper half of the outermost ray there is an elongate pelvic splint bone. The anterior end of this pelvic splint lies free in the somatic musculature.

Vertebral column. The vertebral column is composed of 68 vertebrae. There are 19 caudal vertebrae.

Each centrum is amphicoelous and pierced centrally for the passage of the notochord. The majority of the centra are as deep as long but those anteriorly are deeper than long while those posteriorly are slightly longer than deep. The centra are marked laterally by fine grooves separated by equally fine ridges. The neural arches, haemal arches and parapophyses are received within shallow pits upon the centra.

Anteriorly the neural arches are wide and expanded distally. Towards the posterior end of the abdominal region the neural arches become more slender and there is no distal expansion. The neural spines of the first 34 vertebrae remain as separate halves but posterior to this level the lateral halves fuse to form solid median spines. The neural spines of the third, fourth and fifth preural centra are somewhat longer and straighter than those immediately in front and aid in the support of the caudal fin-rays.

The first 47 centra bear parapophyses. To these are attached the pleural ribs. The anterior parapophyses are small but those associated with centra 35–47 gradually increase in length. Behind this level complete haemal arches and spines are seen, the last four being long and stout and involved in the support of the caudal fin-rays.

Epineural intermuscular bones are only absent from the centrum incorporated into the neurocranium and the last three caudal vertebrae. The epineurals associated with the first 30 or so vertebrae are attached to the bases of the neural arches. Those behind lie free, the anterior free members having forked bases. Epipleural intermusculars are found throughout the caudal region. All lie free, and like their neural counterparts those found anteriorly show forked bases.

Sigmoid supraneurals occur between the tips of the first 32 neural spines. The first supraneural is the largest, thereafter they decrease in size posteriorly. It is of interest to note that supraneurals occur between the first few pterygiophores of the dorsal fin.

Median fins. The dorsal fin lies in the centre of the back and consists of 25 fin-rays of which the first four, although paired, are unbranched and not articulated. The seventh ray is both the longest and the first branched of the series. The fin-rays are supported upon 21 pterygiophores of which all except the first two consist of distinct proximal, middle and distal radials. The distal radials lie between the bases of the fin-rays. The first two pterygiophores consist of two radial elements, fusion having occurred between the proximal and middle radial. Together, the first two pterygiophores support the first five fin-rays.

The origin of the anal fin is midway between the pelvic fin and the caudal peduncle. The anal fin is composed of 17 fin-rays of which the first three are not articulated. The sixth ray is both the longest and the first branched of the series. Thirteen pterygiophores support the fin-rays. The first is long and like its dorsal counterpart consists of fused proximal and median radials and a separate distal radial. The first two pterygiophores support the first six fin-rays.

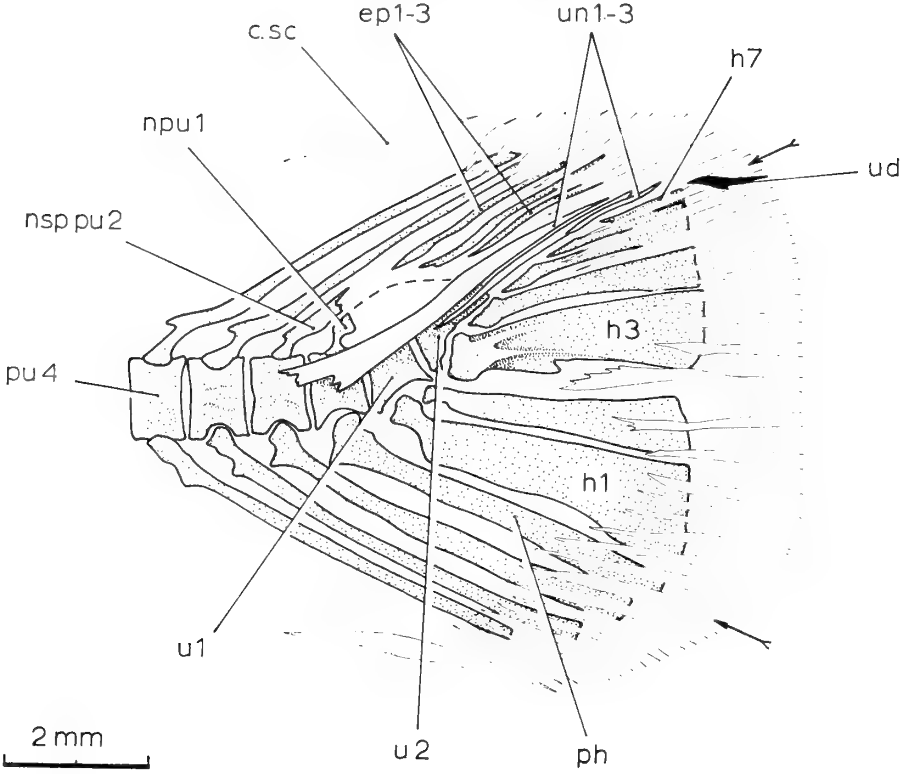

FIG. 10. *Elops hawaiensis* Regan. Caudal skeleton in left lateral view. Arrows indicate upper and lower principal fin-rays.

The caudal fin skeleton of *Elops* has been figured and described several times, the most important references being those of Regan (1910), Hollister (1936) and Nybelin (1963, 1971) and although those works were concerned with *Elops saurus*, *E. lacerta* and *E. senegalensis*, the caudal structure of *E. hawaiensis* is very similar (Text-fig. 10).

Squamation. There are 95–97 scales in the lateral line series. The transverse count immediately in front of the dorsal fin is 12 above and 17 below the lateral line series. The scales are relatively small and approximately circular in shape. The anterior margin tends to be straight. The nucleus is positioned centrally and the surface of the scale is marked by concentric circuli which fade out on the exposed surface. The posterior margin of the scale is often frayed during life giving the margin a crenulated appearance. The anterior field is marked by 9–13 strong radii which interrupt the anterior margin producing a scalloped edge. The scales from the posterior region of the body generally show fewer radii. Bone cells are found within the scales and are most abundant in the anterior fields.

Lateral line scales are distinguished by the presence of a prominent tube containing the lateral line canal. At the bases of the fins there are many smaller scales

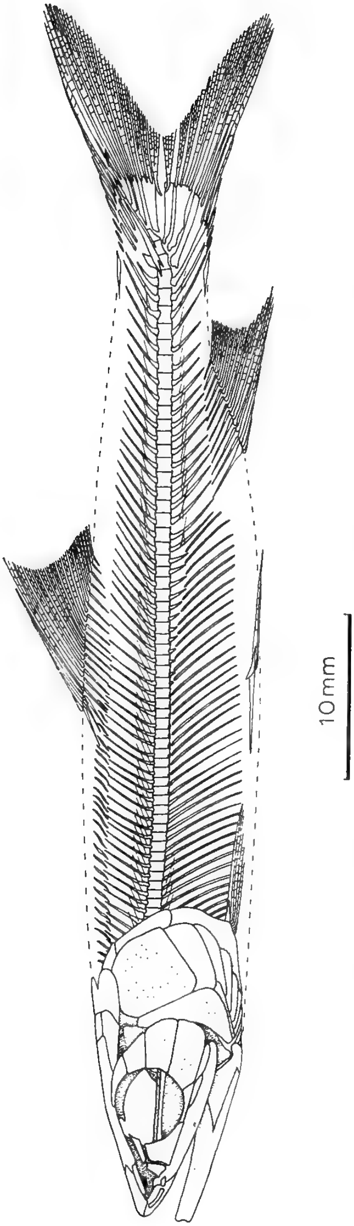

FIG. 11. *Elops hawaiensis* Regan. Entire skeleton, scales omitted.

which tend to be ovoid and to lack radii. Together these small scales form a basal sheath to the dorsal and anal fins. Enlarged axillary scales are present above the paired fins.

Appendix to the genus *Elops*

Woodward (1901) described a fossil form which he referred to the genus *Elops* without any distinct species recognition. The *Elops* sp. is represented by two specimens (B.M.N.H. 39443 and P.1762) from the London Clay (Ypresian) of Sheppey, Kent, England. Unfortunately the specimens are poorly preserved and have suffered from pyritization so that very little may usefully be added to Woodward's (1901) description. *Elops* sp. is certainly larger than any extant species and shows a depression upon the skull roof. This latter feature, although obvious, is of little use taxonomically since the largest individuals of the extant species also show a depression of limited size. The scales of the Eocene *Elops* are marked in their exposed portion by ridges, but again this is sometimes seen in the Recent species. All features that may be seen of the cranial anatomy, vertebral column and squamation suggest that this species is correctly referred to the genus *Elops* but lack of material results in the Eocene form being left as *Elops* sp.

Genus ***DAVICHTHYS*** nov.

Diagnosis. Elopid fishes reaching 120 mm S.L. Head shallow, the length of the cranium forming about 30 per cent S.L. Cranial bones generally smooth. The first infraorbital is rounded and fails to contact the supraorbital. Infraorbital canal with a few moderately long branches ; the union of the antorbital and infraorbital canals not enclosed by bone. Maxilla extending to the hind margin of the orbit ; two supramaxillae, the posterior marked by a pronounced strengthening ridge. Quadrate with the anterior margin considerably longer than the posterior margin ; quadrate/mandibular articulation well behind the eye. Ceratohyal solid. Preoperculum narrow throughout, the contained sensory canal opening directly to the surface by a few large pores. Vertebral column with 50–56 vertebrae of which 20 are caudal. Pectoral and pelvic fins each composed of 12 rays. Scales small, circular and those in the anterior region of the body marked by four or five weakly defined anterior radii.

Remarks. The genus is founded on the best known species, *Davichthys dubius* (Davis) which had been questionably placed in synonymy with *Osmeroides gracilis* Davis, to which it shows little similarity. *O. gracilis* is made the type-species of a new albulid genus *Lebonichthys* on p. 171. *Davichthys* is known from the Lower Cenomanian of Morocco and from the Middle Cenomanian and the Upper Santonian of Lebanon.

Type species. *Osmeroides dubius* Davis.

Davichthys dubius (Davis)

(Text-figs. 12, 13)

1887 *Osmeroides dubius* Davis : 565, pl. 31, fig. 4.
1901 ?*Osmeroides gracilis* Davis ; Woodward : 16.

DIAGNOSIS. *Davichthys* reaching 70 mm S.L. Skull roof with faint ornamentation on the frontal bones above the orbit. Maxilla with straight oral margin ; supramaxillae large ; premaxilla shallow, forming about one-quarter of the oral margin of the jaw. Preopercular sensory canal running at the anterior margin of the bone. Dorsal fin situated in the centre of the back and composed of 15 rays. Anal slightly nearer to the caudal peduncle than to the pelvic fin and composed of 16–17 rays. Caudal fin with fringing fulcra.

HOLOTYPE. Nearly complete fish, R.S.M. 1891.59.38, from the Upper Santonian of Sahel Alma, Lebanon.

MATERIAL. The holotype and the following specimens were examined : R.S.M. 1891.59.147, B.M.N.H. 48155 and 46539. All are from the Upper Santonian of Sahel Alma, Lebanon.

DESCRIPTION. The anatomy of *Davichthys* is very like that of *Elops* and *Anaethalion* and distinguishing characters are few and minor. In several respects *Davichthys* is intermediate between *Elops* and *Anaethalion.*

The head, as in all elopids, is relatively shallow and the gape moderately large. The skull roof is similar to *Elops* and *Anaethalion* in being flat, with medially united parietals and with frontals which are narrow and parallel-sided above the orbit but widen considerably above the otic region. In contrast to *Elops* and *Anaethalion* the frontal of *Davichthys* is ornamented above the orbit by weak ridges. The dermethmoid is flat, as in all elopoids, and does not bear the ventro-lateral projections seen in some species of *Anaethalion* (Nybelin 1967b : fig. 4B). The absence of such projections is a resemblance to *Elops.* An ethmoid commissure could not be identified in the specimens examined.

The neurocranium is shallow with the narrow, straight parasphenoid lying almost horizontally, as in other elopids. Anteriorly the vomer bears a rounded tooth plate which carries a dentition of small pointed teeth. Whether the vomerine tooth plate was paired or not could not be seen.

The hyomandibular is attached to the neurocranium by a single broad head and the shaft is inclined posteriorly, as in *Elops* and some species of *Anaethalion.* While most elopids have an undivided hyomandibular head *Elops saurus* shows a clear division into anterior and posterior portions (cf. Ridewood 1904 : fig. 10).

The metapterygoid overlaps both the hyomandibular and the endopterygoid and is unusual among elopids in being deeper than long. The quadrate is also distinctive in that the anterior border is longer than the posterior. As in *Elops* and *Anaethalion* the quadrate does not have a well-defined facet behind the articulatory condyle as it does in megalopids. In the remainder of the hyopalatine series there is a close similarity with other elopids. Thus the ectopterygoid is narrow and shows a ridge

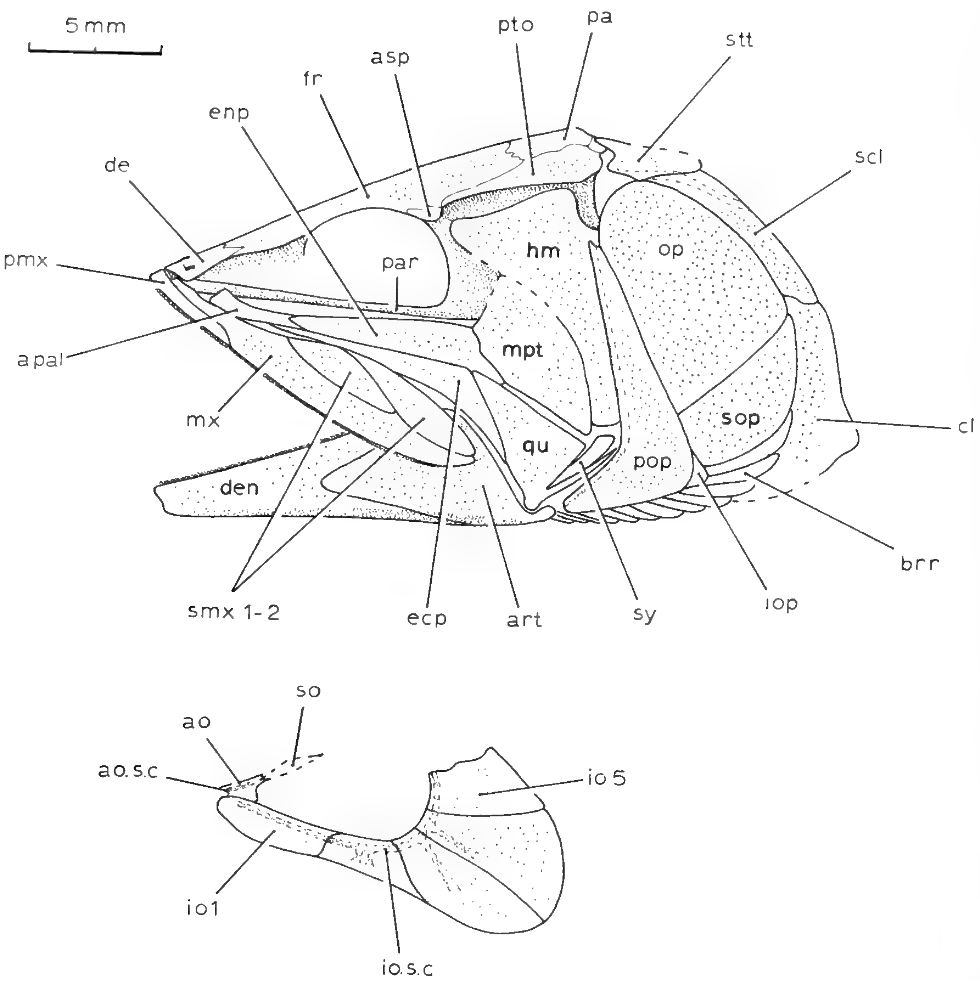

FIG. 12. *Davichthys dubius* (Davis). Above, cranium in left lateral view. Below, circumorbital bones. Restoration based on several specimens.

which probably represents a rudimentary ectopterygoid process and the ectopterygoid, endopterygoid and dermopalatine bear many tiny teeth. The autopalatine is weakly ossified and the anterior end is produced in a simple rounded knob.

The upper jaw is like that of other elopids. The premaxilla is narrow compared to that bone in *Elops* and the maxilla, which is deeper than that of *Elops*, bears an ill-defined palatine process. This small palatine process is more like the bony nubbin seen in *Anaethalion* than the well-developed process in *Elops*. There are two supramaxillae, the posterior of which bears a prominent strengthening ridge as in *Anaethalion*. The dentition of the upper jaw consists of a band of tiny pointed teeth on both the maxilla and premaxilla.

The mandible is similar to that of other elopids in being shallow throughout with a small coronoid process situated posteriorly and in having the mandibular sensory

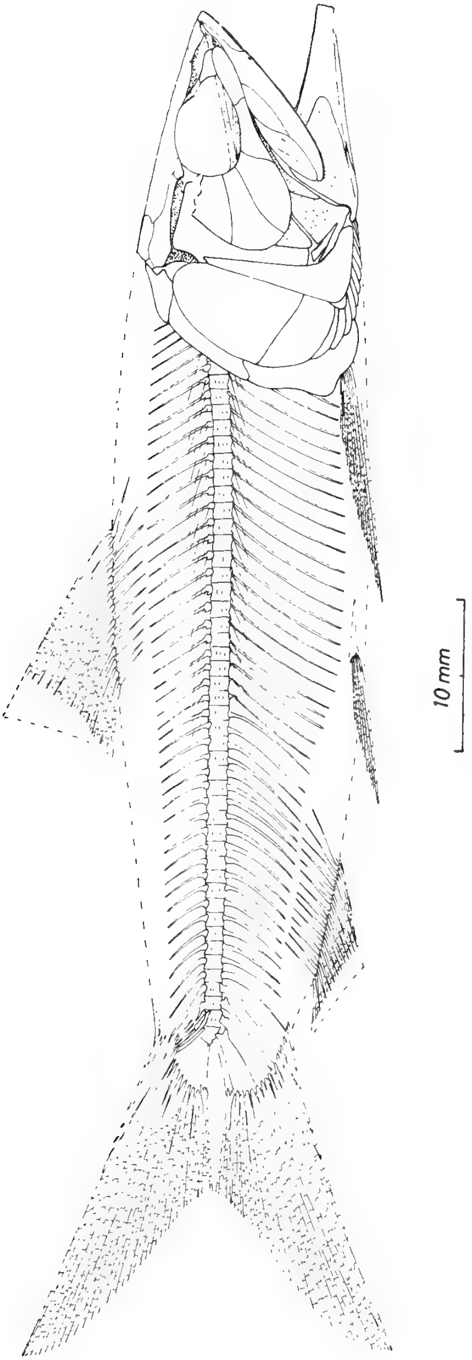

FIG. 13. *Davichthys dubius* (Davis). Entire skeleton, scales omitted. Based on R.S.M. 1891.59.147.

canal wholly contained within bone. The oral margin of the dentary is straight, unlike the concave outline of the dentary of *Elops*. The dentition is similar to that of *Elops*. The quadrate/mandibular articulation occurs beneath the otic region.

The bones surrounding the orbit are set in typical elopid fashion. The nasals are slender tubes which probably lay free in the skin. The splint-like supraorbital lies in tandem with the triangular antorbital. Five infraorbitals were recognized but a dermosphenotic was not seen. The first infraorbital is rounded anteriorly as in *Anaethalion* and thus differs from the *Elops* condition. In shape the posterior infraorbitals are very similar to those of other elopids, but in their width there is a closer resemblance to *Elops*. The infraorbital sensory canal runs close to the orbital margin and sends off bone-enclosed branches within the second, third and fourth infraorbitals. These bone-enclosed branches are a resemblance to *Anaethalion* rather than *Elops*. Anteriorly the main infraorbital canal passes straight out of the bone. The narrow antorbital branch must have linked with the infraorbital canal outside the bone, as in *Elops* but unlike *Anaethalion* (Nybelin 1967b).

The anterior and posterior ceratohyals are the same shape as in *Elops* and extend between the jaw rami. As in *Elops* the anterior ceratohyal is solid, not fenestrated as it is in *Anaethalion*. Little may be seen of the branchial arches, but the first and second gill arches bore long gill-rakers, a feature which is totally unlike *Lebonichthys* (=*Osmeroides*) *gracilis* to which *Davichthys dubius* had previously been allied.

The opercular series is very much like that of *Anaethalion*. The preoperculum is narrow throughout, unlike *Elops*, but like that genus the sensory canal runs at the anterior margin in contrast to the condition in *Anaethalion*.

The postcranial skeleton is little different from either *Elops* or *Anaethalion*. The vertebral column consists of 50 vertebrae of which approximately 19 are caudal. The total count agrees more closely with *Anaethalion* (42–66) than with *Elops* (63–80) but in all three genera there are approximately the same number of caudal vertebrae.

The dorsal fin is situated in the middle of the back as in *Elops* but unlike most species of *Anaethalion* except *A*. ?cf. *subovatus* (Nybelin 1967b : pl. 5).

A distinction from both *Elops* and *Anaethalion* is the length of the pectoral fin-rays, which extend posteriorly almost to the pelvic fin.

The caudal skeleton is, as far as may be seen, similar to both *Elops* and at least some species of *Anaethalion*. In retaining fringing fulcra there is a greater similarity with *Anaethalion*.

The cycloid scales are small, circular and marked by fine circuli. Those in the anterior region of the body have three or four radii in the anterior field which produce a scalloped anterior margin.

Davichthys gardneri sp. nov.

(Text-figs. 14, 15)

DIAGNOSIS. *Davichthys* reaching 120 mm S.L. Skull roof without ornament. Maxilla with straight oral border ; supramaxillae slender, the second particularly shallow posteriorly. Premaxilla forming nearly one-third of the upper jaw margin

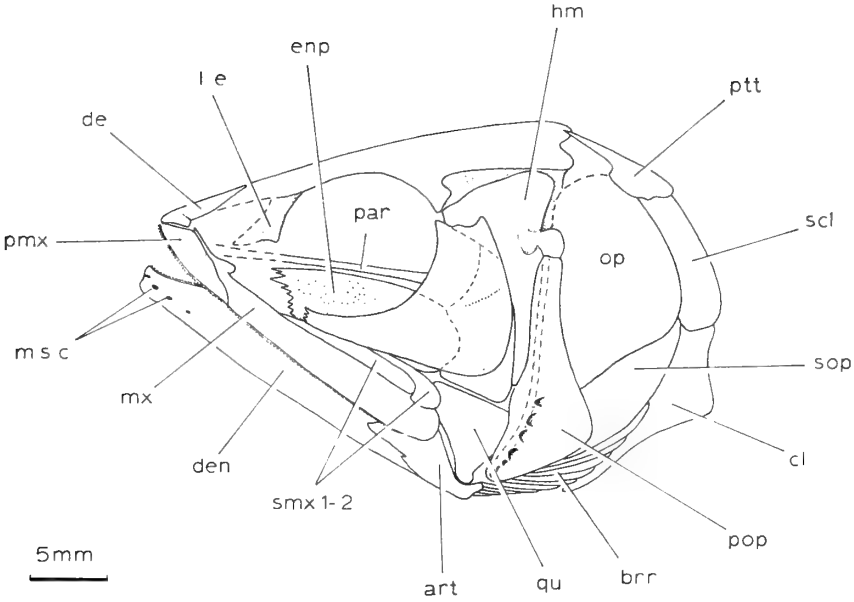

FIG. 14. *Davichthys gardneri* sp. nov. Cranium and pectoral girdle in left lateral view. Based on the holotype.

and moderately deep anteriorly. Preopercular canal distant from the anterior margin of the bone. Dorsal fin situated mid-way between the occiput and the caudal peduncle and composed of 23 rays. Anal situated mid-way between the pelvic fin and the caudal peduncle, with 14 rays. Fringing fulcra absent.

HOLOTYPE. Nearly complete fish, B.M.N.H. 49520, from the Middle Cenomanian of Hakel, Lebanon.

MATERIAL. No material other than the holotype is known.

REMARKS. This species is founded on a single specimen previously identified as *Halec*. The essential characters of the genus *Davichthys* are to be found here, the differences from the type-species being those meristic counts and morphometric ratios which may be inferred from the specific diagnoses.

Davichthys gardneri is larger than the type-species and has a relatively deeper head. The dermethmoid is produced laterally as a small prong resembling the larger process in *Anaethalion*.

The hyomandibular of *D. gardneri* shows a very well-developed opercular process and the shaft is narrow, differing in both features from *D. dubius*. The upper jaw differs from that in the type-species in showing a prominent palatine process on the maxilla, very shallow supramaxillae and a premaxilla which is substantially deeper.

The preoperculum appears slightly more primitive than in the type-species, having no lower limb and the sensory canal distant from the anterior margin. The

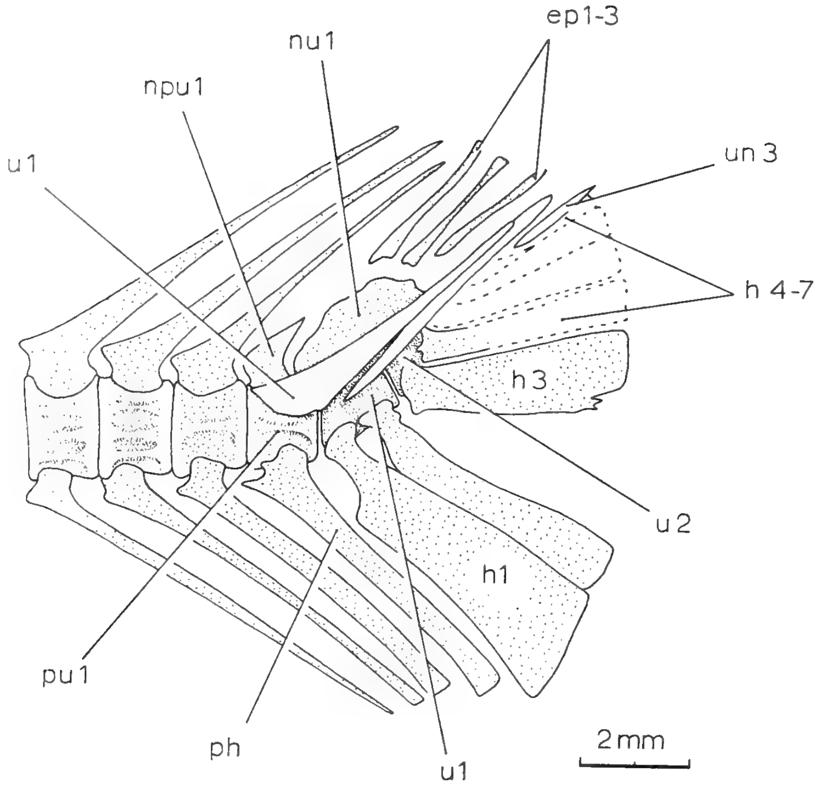

FIG. 15. *Davichthys gardneri* sp. nov. Caudal skeleton in left lateral view. Based on holotype.

operculum is narrower than in *D. dubius* and the ventral margin shows a slight indentation.

Little observable difference exists in the postcranial skeleton, except for the meristic counts. The caudal fin does not bear fringing fulcra which are present in the type-species.

Davichthys lacostei (Arambourg)

1954 *Holcolepis lacostei* Arambourg : 54, text-figs. 28, 29, pl. 7, figs, 1, 3, 4.

DIAGNOSIS (emended). *Davichthys* reaching 90 mm S.L. Skull roof smooth. Maxilla with convex oral margin, both supramaxillae large and rounded, premaxilla small. Preopercular sensory canal distant from the anterior margin of the preoperculum. Dorsal fin nearer to the caudal peduncle than the occiput and composed of 14 rays. Anal slightly nearer to the caudal peduncle than the pelvic fins and composed of 9 rays.

FORMATION AND LOCALITY. Lower Cenomanian of Jebel Tselfat, Morocco.

REMARKS. This species has been described in some detail by Arambourg (1954). The chief differences from the other species concern the position and size of the median fins, the shape of the maxilla and the small size of the premaxilla. *D. lacostei* shares with *D. gardneri* a similarly shaped hyomandibular, an unornamented cranial roof and a similarly disposed preopercular sensory canal.

Remarks on the genus *Davichthys*

The close resemblance of *Davichthys* to other elopids has necessitated nothing more than the above comparative notes. Removal of the type-species from association with *Lebonichthys gracilis* is justified by the lack of any of the albulid specializations characterizing *Lebonichthys* (p. 171).

A new genus is made for these three species because they are intermediate in structure between the Upper Jurassic *Anaethalion* and the Eocene–Recent *Elops*. *Davichthys* appears to be the sole Cretaceous representative of the family Elopidae.

Genus ***ANAETHALION*** White, 1938

(Text-figs. 16–19)

For generic synonymy see Gaudant (1968). For diagnosis of the genus see Nybelin (1967b).

The genus *Anaethalion* as now understood is constituted by several Upper Jurassic (Kimmeridgian) species from Germany, France and Spain. The genus was first described by Munster (1842a) who used the preoccupied name *Aethalion* for his type-species, *A. angustus*. New species were added and described by Munster (*op. cit.* and 1842b), Winkler (1862) and Wagner (1863). Sauvage (1903) recognized two species (*A. vidali* and *A. gigas*) from Lérida, Spain.

Nybelin (1967b), in a taxonomic revision of the genus as represented in the Kimmeridgian of Germany, recognized five (possibly six) species, viz. ; *A. angustus* (Munster), *A. angustissimus* (Munster), *A. knorri* (Blainville), *A. mayri* Nybelin, *A.* sp. and *A.* (?) cf. *subovatus* (Munster). Lack of cranial material cast doubt on the inclusion of the last-mentioned species in the genus. Gaudant (1968) revised the species from France and came to the conclusion that in addition to *A. knorri* and *A. angustus* there were also two different species ; *A. affinis* Gaudant and *A. cirinensis* Gaudant. Both Nybelin (1967b) and Gaudant (1968) have described the anatomy of *Anaethalion*.

The purpose of the present work is to evaluate the relationships of the genus, primarily upon the basis of the anatomy of *Anaethalion vidali*. No attempt is made to analyse the validity of the species recognized hitherto as the author has only had the chance to examine a limited amount of material. The material examined is as follows : *Anaethalion angustus*, B.M.N.H. 37926, 37912, 37927 ; *A. knorri*, B.M.N.H. 36030, 37903, 37839, 37042, P.1095 ; *A. angustissimus*, B.M.N.H. P.3575, 37901 (neotype) ; *A.* (?) cf. *subovatus*, B.M.N.H. P.3656, P.3723 ; *A.* sp., B.M.N.H. P.3728, 37048 ; *A. gigas*, B.M.N.H. P.10927, P.10377, P.10380 ; *A. vidali*, B.M.N.H. P.10375 and P.10376.

Anaethalion has been referred to the Leptolepididae by Woodward (1895), Berg (1940), Bertin & Arambourg (1958), Danil'chenko (1964) and Romer (1966). Nybelin (1967b) did not firmly suggest a familial position although he hinted strongly at a relationship with *Elops*. Similarly Gaudant (1968) could not reconcile *Anaethalion* with the Leptolepididae and erected a new family, the Anaethalionidae.

I would agree with both Nybelin and Gaudant that *Anaethalion* should be excluded from the leptolepids. There are several features of dissimilarity from leptolepids which, at the same time, are points of similarity with *Elops*. The neurocranium is shallow ; there is a connection between the supraorbital and infraorbital sensory canals ; the supratemporal bone is large (unlike Upper Jurassic leptolepids) ; the infraorbital and preopercular sensory canals show few branches ; there is no basipterygoid process ; both the maxilla and dentary are shallow, the latter bearing only a weakly defined coronoid process posteriorly ; and the dentition upon the dermal jaws consists of broad bands of villiform teeth.

Although *Anaethalion* is unlike leptolepids, it must also be said that definite evidence of elopid affinity is lacking for most species of *Anaethalion*. It is true that *Anaethalion* is most favourably compared with *Elops* and *Davichthys*, but a positive association with elopids could only be made on finding rostral ossicles, an associated leptocephalus larva or a pectoral splint. A pectoral splint is present in *Anaethalion vidali* and consequently this form may be assigned to the Elopidae with some degree of certainty (but see footnote p. 190). The other species may or may not be elopids. In caudal anatomy there is some variability from species to species within the genus *Anaethalion*. These caudal variations and their possible implications in understanding the relationships of *Anaethalion* species are discussed below (p. 39).

The following remarks on the genus are based primarily on *A. vidali*, the only species definitely referable to the Elopidae.

To describe the anatomy of *A. vidali* would essentially be a repetition of the description given for *Elops*, so alike are the two forms. The differences that exist are minor and many are bridged by *Davichthys*.

The skull roof of *Anaethalion* differs from that of *Elops* only in the form of the dermethmoid, which bears ventro-laterally directed processes similar to those seen in young *Tarpon* and *Megalops*. Such horns are absent in *Elops* but may be seen in *Davichthys gardneri* and probably represent a primitive teleostean condition.

Little is known concerning the neurocranium of any species of *Anaethalion*. What is known suggests that the neurocranium is primitive, closely resembling that of *Elops*. Within the otic region the pars jugularis is long with separate openings as in *Elops*, the subtemporal fossa is deep and there is a prootic-intercalar bridge in at least *A. vidali* and *A. knorri*. Posteriorly the first vertebral centrum is incorporated with the neurocranium (also figured for *A. knorri* by Nybelin 1967b) and this centrum bears a large neural arch.

The snout of *A. vidali* resembles that of *Elops* ; the mesethmoid must have been unossified and the lateral ethmoid is represented by a thin sliver of perichondral bone. Although the shape of the vomer could not be seen it is known to be a short element bearing many small villiform teeth. Other species of *Anaethalion* examined show a comparable development of the vomer and lateral ethmoid although most appear to show some endochondral ossification of the mesethmoid.

In all species of *Anaethalion* the parasphenoid is relatively narrow throughout and is without a basipterygoid process. *A. vidali* differs from most species of the genus, and also from *Elops*, in the shape of the parasphenoid. In *A. vidali* the parasphenoid is angled beneath the ascending wings. At this same level there are slight lateral swellings. Both of these features are seen in the parasphenoid of megalopid fishes and the shape of this element in *A. vidali* (Text-fig. 16, par) is most favourably compared with that of *Tarpon* (Text-fig. 23, par). Small villiform teeth are borne on the parasphenoid.

Anaethalion vidali differs from other species of *Anaethalion* examined in having the otic region of the neurocranial roof convex and the autosphenotic spine well developed (Text-fig. 16, asp).

The hyopalatine series is of the basic teleostean plan (Text-fig. 16). Unlike *Davichthys* the metapterygoid is relatively shallow and thus more closely resembles that seen in *Elops*. There is no evidence of an ectopterygoid process but the dorasl margin of the ectopterygoid is slightly thickened. The quadrate/mandibular articulation occurs beneath the posterior border of the eye, as in most other species of *Anaethalion*, and is in a similar position in *Davichthys lacostei* (Arambourg 1954: fig. 28). In other species of *Davichthys* and *Elops* the articulation is situated more posteriorly. *A. angustissimus* shows a condition similar to *Elops*. The backward movement of the quadrate/mandibular articulation is a trend to be noted in the Elopidae.

The upper jaw of *A. vidali* is similar to that of other elopids, showing a small premaxilla and small supramaxillae, the latter proportionately smaller than in *Elops* and *Davichthys*. The palatine process on the maxilla is relatively small in *Anaethalion*. Most species of *Anaethalion* (but not *A. vidali*) show a stout strengthening ridge upon the posterior supramaxilla, a feature which is interpreted as being the primitive condition.

The lower jaw is shallow as in other elopids and although other species of *Anaethalion* show a variation in the depth and shape of the mandible (see Nybelin 1967b) all show a weakly defined, posteriorly situated coronoid process, in contrast to leptolepids.

The anterior ceratohyal of all examined species of *Anaethalion* is fenestrated, unlike that of *Davichthys* and *Elops*. A fenestrated ceratohyal is probably a primitive feature since it is found in a great many primitive teleosts.

The circumorbital series of *A. vidali* is not known but there are minor differences between other species of *Anaethalion* and *Elops*. The circumorbital series of several species of *Anaethalion* has been described and figured by Nybelin (1967b) and Gaudant (1968). In those species of *Anaethalion* known in this respect the first infraorbital is ovoid, with a triangular antorbital resting directly upon its antero-dorsal margin. There is no connection between the lachrymal and the supraorbital, and the triradiate division of the infraorbital sensory canal (i.e. the origin of the antorbital

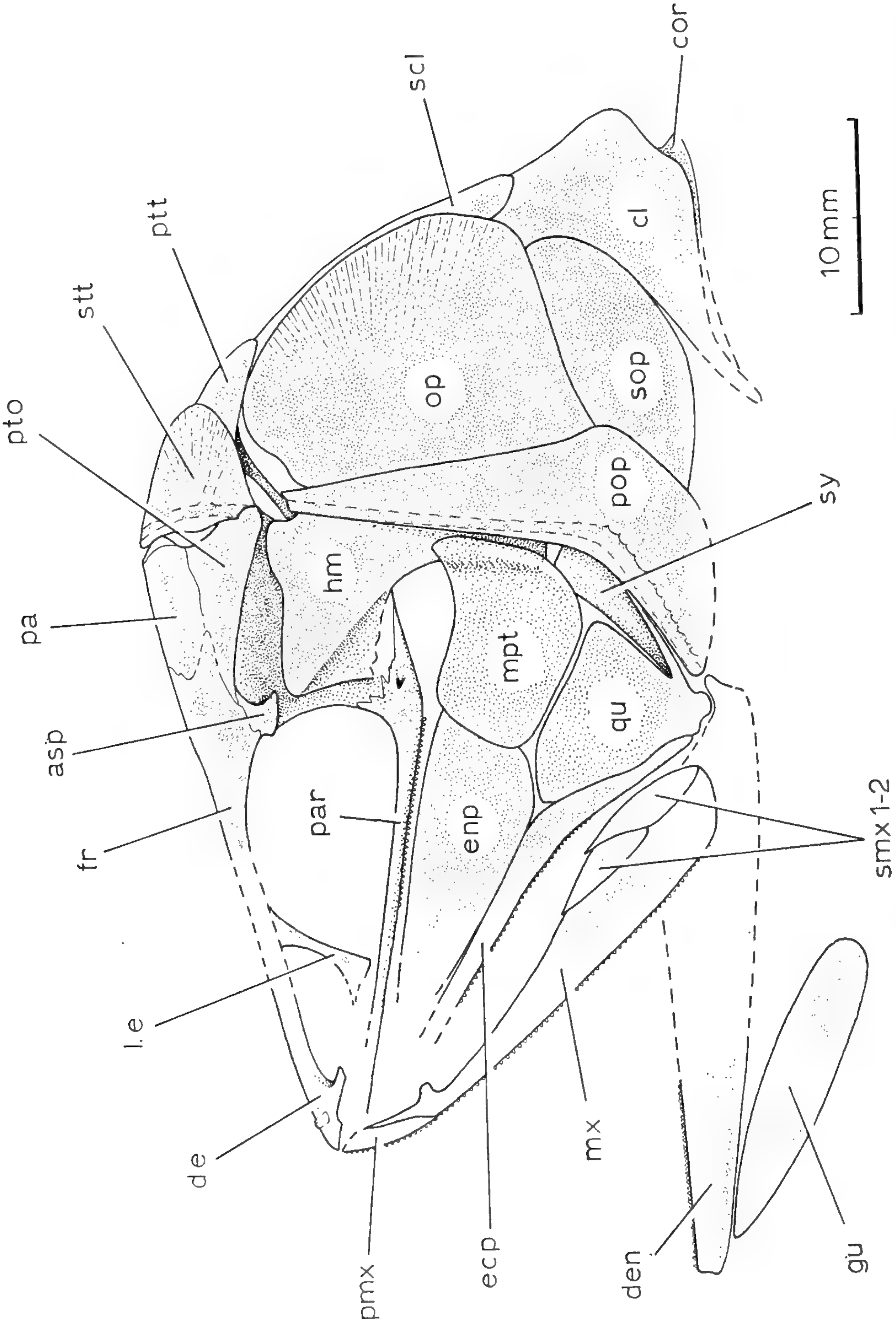

FIG. 16. *Anaethalion vidali* (Sauvage). Cranium and pectoral girdle in left lateral view. Based on B.M.N.H. P.10375.

and ethmoid commissure branches) lies within the lachrymal. In *Elops* the lachrymal is elbowed and contacts the supraorbital dorsally, the splint-like antorbital lying along the anterior margin of the upright limb. The triradiate division of the infraorbital sensory canal occurs in the skin anterior to the lachrymal. Junction of the lachrymal and supraorbital bones, so excluding the antorbital from the orbital margin, is rare in lower teleosts, although it has been figured for *Leptolepis dubia* (Patterson 1967a: fig. 4) and is therefore of doubtful phyletic significance. The bone-enclosed branches of the infraorbital sensory canal of *Anaethalion* are similar to *Davichthys* but unlike *Elops*.

The preoperculum of *A. vidali* and other species of *Anaethalion* consists essentially of a vertical limb, the horizontal portion being short. *Elops*, *Davichthys dubius* and *D. lacostei* show a more pronounced horizontal limb and the preoperculum is slightly expanded postero-ventrally. The preopercular sensory canal of all species of *Anaethalion* opens to the surface within the lower portion of the bone. In *A. vidali*, as in other elopids, the main canal opens directly to the surface via a series of pores but in other species of *Anaethalion* there are a few well-developed secondary branches enclosed within the bone. The latter condition is considered the more primitive.

The postcranial skeleton of *A. vidali* is similar to that of *Elops*, with no significant differences in the vertebral column or the paired fins and girdles. The vertebral count of *A. vidali* (66) is substantially higher than that of most species of *Anaethalion* (range 42–57).

In most species of *Anaethalion* the dorsal fin, although of the same shape and size as the dorsal of *Elops*, is situated slightly nearer to the caudal peduncle than the occiput. In *Elops* the dorsal is situated in the centre of the back. Among the species of *Anaethalion*, *A.* (?) cf. *subovatus* and *A. vidali* show an *Elops*-like disposition of the dorsal fin. *A. vidali* exhibits three features of the fins normally associated with megalopids among Elopiformes: the origin of the pelvic is in advance of that of the dorsal, the anal fin is slightly elongated and the first anal pterygiophore is stout and long, nearly touching the vertebrae above.

The caudal skeleton of *A. vidali* (Text-fig. 17) is very similar to that of *Elops* (or, for that matter, later leptolepids) the main difference being the development of a complete neural spine associated with the second preural centrum. However, a complete neural spine upon the second preural centrum is also seen in *Davichthys gardneri* among elopids. Unlike *Elops*, *A. vidali* shows a single fringing fulcrum, a structure which is also seen in *Davichthys dubius*. *Anaethalion vidali* differs from other elopids but resembles some other species of *Anaethalion* in the development of laminar bone on the anterior margins of the third and fourth preural neural spines.

The caudal skeleton of the German species of *Anaethalion* shows several variations from that of *A. vidali*. Sketches of some of these species are given in Text-fig. 18 (see also Nybelin 1971). The development of laminar bone varies; it is well developed in *A. knorri*, *A. angustus* and also in the Spanish *A. gigas*; *A. angustissimus* shows weakly developed laminar bone on the second preural neural spine and as in *A. knorri* and *A. angustus* there are well developed projections at the bases of the first few preural neural and haemal spines.

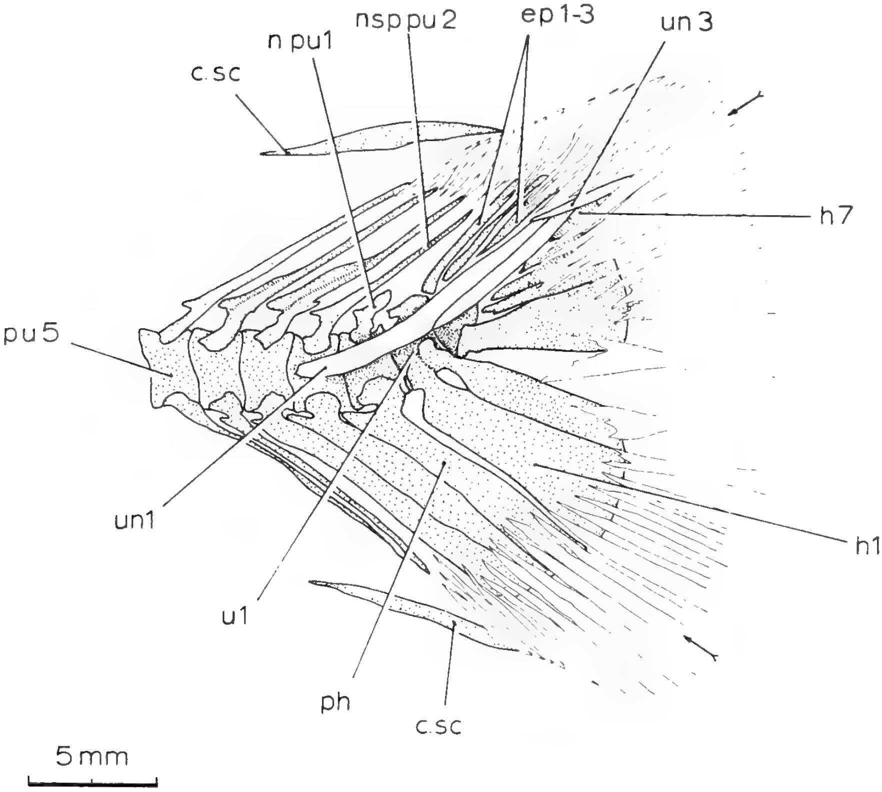

FIG. 17. *Anaethalion vidali* (Sauvage). Caudal skeleton in left lateral view. Camera lucida drawing of B.M.N.H. P.10375, partially restored. Arrows indicate upper and lower principal fin-rays.

There is also variation in the length of the second preural neural spine, long in *A. angustus*, ' three-quarter length ' in *A.* (?) cf. *subovatus* and ' half-length ' in *A. angustissimus*, *A. knorri*, *A. gigas* and *A.* sp.

The three epurals of most species of *Anaethalion* form a graded series but those of *A. angustissimus* are subequal in length, as in many primitive euteleostean fish.

It is also to be noted that *A. gigas* from the Kimmeridgian of Spain shows a large neural structure above the first preural and first ural centra. This appears to be a result of fusion between two neural arches which in other species remain separate. Such a fused structure may be a function of size.

Regrettably, too few specimens were examined to allow an assessment of these variations. The neural arches and spines are known to vary in *Megalops* (Text-fig. 33) and perhaps little attention is justified. The development of laminar bone in some species may be of significance since this feature is usually associated with the euteleostean caudal skeleton (Patterson 1970b).

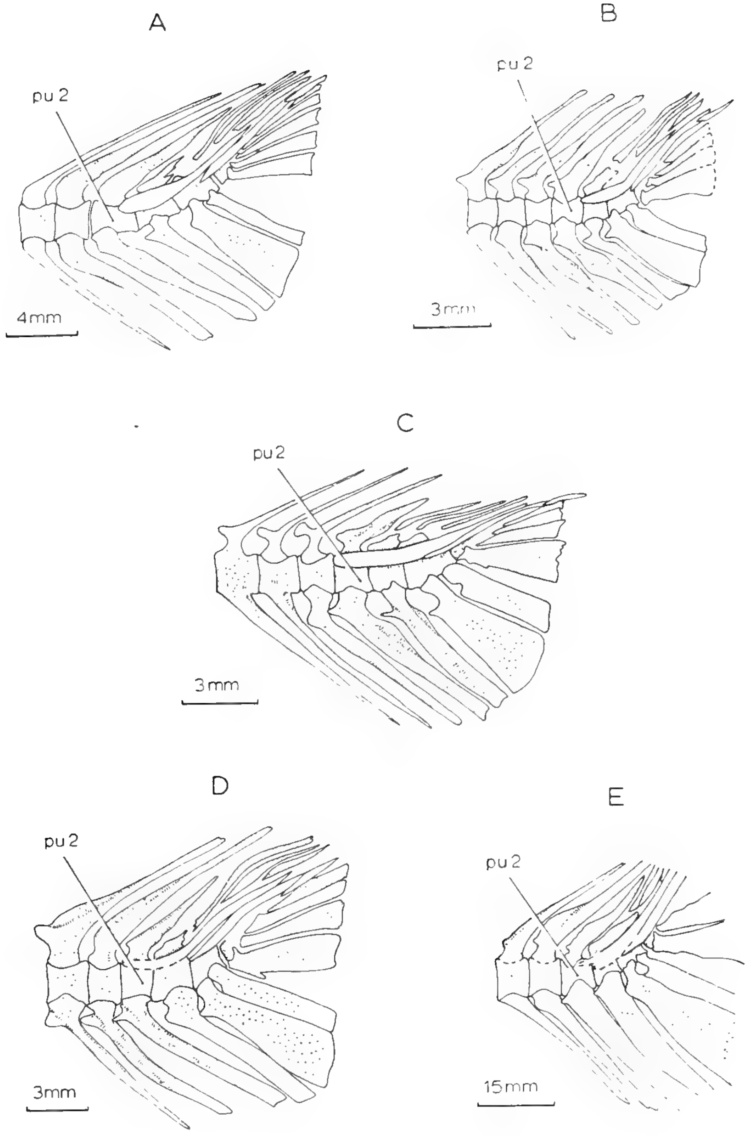

FIG. 18. *Anaethalion.* Caudal skeletons of various species. Based on camera lucida drawings. A. *Anaethalion* (?) cf. *subovatus* from B.M.N.H. P.3723; B. *A. angustus* from B.M.N.H. 37927; C. *A. angustissimus* from B.M.N.H. 37901; D. *A. knorri* from B.M.N.H. 37839; E. *A. gigas* from B.M.N.H. P.10380. A to D have been reversed.

The variations in the caudal skeleton of *Anaethalion* illustrated by Nybelin (1963, 1967b, 1971) and here (Text-fig. 18) do not, however, encompass the type shown by Gaudant (1968 : fig. 5) for *A. cirinensis*, based on the holotype (Gaudant *op. cit.* pl. 3, fig. 2). The figure given by Gaudant is unusual for two reasons ; a complete neural arch and spine is shown on the first preural centrum and the third uroneural is elongate and overlaps the second ural centrum. Both these conditions are not met with in elopid (or late leptolepid) fishes, but are usually associated with osteoglossomorph fishes (cf. *Hiodon* and *Lycoptera* as figured by Greenwood 1970b).

From the plate given by Gaudant the apparent discrepancy between his drawing and other species of *Anaethalion* may be reconciled. The neural structure borne by the first preural centrum appears to represent a neural arch only, there being no indication, even as an impression, of a distal prolongation. The uroneural structure is correctly figured as may be seen by comparing the plate and drawing and inasmuch as there are three visible uroneurals the labelling is accurate. However, the third uroneural figured by Gaudant probably represents the second of other *Anaethalion* species and elopoids. In length and proximal extension this uroneural is exactly comparable with the second uroneural of elopoids and other species of *Anaethalion*. Presumably the third uroneural is either missing from the specimen or possibly represented by the splint-like structure shown below the distal extremity of the ' third ' uroneural (Gaudant 1968 : pl. 3, fig. 2). The first two uroneurals (U_1 and U_2 of Gaudant 1968 : fig. 5) represent the unfused condition of the first uroneural of elopoids which is known to be a compound element. Thus the first two uroneurals of *A. cirinensis* resemble those of leptolepids.

The scales of *Anaethalion* (unknown in *A. vidali*) are moderately large, circular and marked by fine circuli which are absent from the central portion of the exposed field. Bone cells are present. Such features are similar to those of *Elops*. However, the scales of *Anaethalion* do not show the well-marked anterior radii characteristic of all elopiforms.

In summary, the genus *Anaethalion* is an assemblage of primitive teleostean fishes most favourably compared with the Elopidae. *Anaethalion* is more advanced than known leptolepids in showing a reduction of the ethmoid ossification and lacking a basipterygoid process. The suspensorium and dermal jaws are primitive as are many features of the neurocranium and give no indication as to the relationships of most species of *Anaethalion*. The caudal skeleton is seen to vary from species to species (Nybelin 1971) and it may be of significance that some species show laminar bone, a feature normally associated with euteleosteans. The structure of the caudal skeleton suggests that *A.* (?) cf. *subovatus* and *A.* sp. are closely related ; *A. knorri*, *A. angustus* and *A. angustissimus* are probably interrelated species and may be linked to *A.* sp. and *A.* (?) cf. *subovatus* by *A. vidali*. *Anaethalion cirinensis* appears to be the most primitive species on the basis of caudal anatomy since it shows three long uroneurals, the first two representing a ' pre-fusion ' state compared with other species of *Anaethalion*.

The elopid *A. vidali* resembles the Megalopidae in some respects. Thus the shape of the body, the position of the pelvic fin and the elongate first anal pterygiophore are similar to *Tarpon*. In the cranium the otic region of the cranial roof is convex,

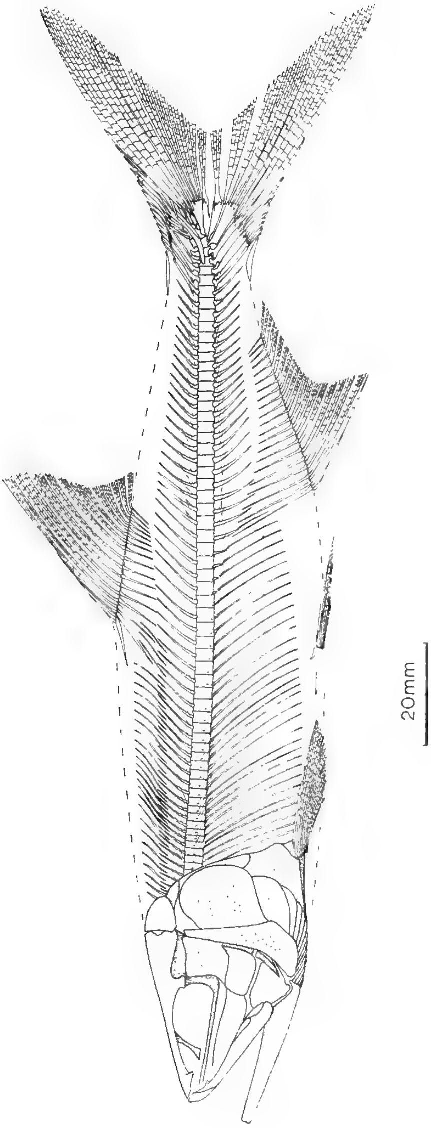

FIG. 19. *Anaethalion vidali* (Sauvage). Entire skeleton, scales omitted. Based on B.M.N.H. P.10375.

the autosphenotic spine is well developed and the dilatator fossa is relatively deep. These features, and the shape of the parasphenoid, are reminiscent of those seen in megalopids. Further research on *A. vidali* may justify the inclusion of this species in the Megalopidae.

Family **MEGALOPIDAE** Jordan, 1923

Diagnosis. Elopoid fishes in which the body is compressed. Cranium deep, mouth terminal or (more usually) superior. Cranial roof convex above the otic region. Parietals without evidence of middle pit-lines. Autosphenotic spine and epiotic process well developed. Post-temporal fossae extend forward to orbitosphenoid and are confluent above the cranial cavity. Dilatator fossa with or without roof. Otophysic connection developed in at least some representatives; intercalar enlarged, partially or completely surrounding the cranial diverticulum of the swimbladder. One rostral ossicle. Quadrate/mandibular articulation beneath orbit. Mandible with prominent coronoid process. Pseudobranchiae present (Holstvoogd 1965). Pelvic fins originating beneath or anterior to the dorsal fin origin. Anal fin slightly elongated (compared with Elopidae). First anal pterygiophore extending to the vertebral column. Urodermal absent. Scales with three to six basal radii, posterior field ornamented. Lateral line tubes branched.

Genus ***TARPON*** Jordan & Evermann, 1896

For full generic synonymy see Hildebrand (1963).

Diagnosis (emended). Megalopid fishes reaching 1800 mm in length. Neurocranial roof markedly convex above the cranial vault. Parietals considerably longer than broad in adult. Dilatator fossa broad, shallow and without a roof. Intercalar not entering the lateral wall of the periotic bulla. Jugular canal opening below the level of the subtemporal fossa. Maximum depth of the neurocranium at the occiput. Maxilla extending behind the eye. Scales with three to four anterior (basal) radii.

Type and only species. *Megalops atlanticus* Cuvier & Valenciennes, 1846.

Tarpon atlanticus (Cuvier & Valenciennes)

(Text-figs. 20–29)

For synonymy see Hildebrand (1963).

Diagnosis (emended). *Tarpon* in which the origin of the pelvic fin is in advance of the dorsal fin. Maximum depth of body less than the length of the head. Dorsal fin with 13–15 rays, anal 22–25. Vertebral column with 53–57 vertebrae of which approximately 20 are caudal. Lateral line with 41–48 scales. Fringing fulcra one to four in number.

Habitat. Atlantic coastal waters of North and South America (from Cape Cod to Brazil), sometimes entering fresh water. Also recorded from tropical West Africa.

There is a great deal of literature on both locality data and growth stages of *T. atlanticus*, a useful synopsis of which is found in Hildebrand (1963).

REMARKS. The skeleton of *Tarpon atlanticus* has never been satisfactorily described. This, and the fact that in several respects it is more primitive than the frequently cited *Megalops cyprinoides* has led to the inclusion here of a more complete account. Omitted details are those of the caudal fin anatomy, which have been dealt with by Hollister (1936 : 263–268), and the otic region of the skull (in so far as this has been affected by the anterior swimbladder diverticula) which has been described by Greenwood (1970a).

DESCRIPTION. In a young individual (*c.* 87 mm S.L.) the cranium is one and a half times as long as deep. Throughout life the depth increases with respect to length. Other morphometric changes that occur during growth are dealt with in the description. Unless otherwise stated, remarks apply to adult individuals.

Neurocranium. The skull roof is flat anteriorly but becomes strongly convex posteriorly. In lateral view the dorsal margin of the skull roof is perfectly straight, or in some large specimens may even exhibit a slight concavity (cf. Gregory 1933 : fig. 31). The greatest width of the neurocranium is equal to 60 per cent of its length and occurs at the sphenotic level. During growth the skull roof becomes relatively wider, due primarily to the development of strong sphenotic spines, and the distance from the occiput to the level of the sphenotic spines increases relative to the total neurocranial length. This differential growth is quite considerable (in a fish of *c.* 87 mm S.L. the distance from the occiput to the level of the sphenotic spines is 26·5 per cent of the total neurocranial length, while in a fish of 650 mm this distance is 37 per cent) and may reflect the development of the enormous post-temporal fossae.

The anterior portion of the skull roof is formed, as in all megalopids, by a complex median dermethmoid. The horizontal part of this bone is constricted one-third of the way back. To the anterior margin of the bone is attached a strong ligament from the head of the maxilla. The ethmoid commissure runs transversely through the tubular rostral, near the anterior border. Laterally, a large pore receives the canal from the lateral rostral. Immediately medial to this, another large pore opens posteriorly and near the mid-line a much smaller pore opens anteriorly. Posteriorly, the dermethmoid overlaps the anterior end of the frontals. A postero-ventrally directed wing arises from beneath the lateral border of the dermethmoid and passes down over the cartilage surrounding the olfactory organ. Posteriorly this wing, in older specimens, is in sutural contact with the lateral ethmoid.

It appears that the lateral processes are ossifications embryonically distinct from the main body of the dermethmoid. Patterson (1970b) states that similar ossifications are present in *Leptolepis coryphaenoides* and *Megalops* and that they are similar to the 'proethmoids' of the stomiatoid *Polymetme*. For a fuller account of the homology of these lateral processes see Patterson (1970b : 261–262).

The frontal is the largest single component of the skull roof. Anteriorly it passes beneath the dermethmoid almost to the anterior end of the latter (Nybelin 1967a : fig. 2C figures the anterior termination of the frontal as lying completely behind the dermethmoid), while posteriorly the frontal overlies part of both the pterotic and

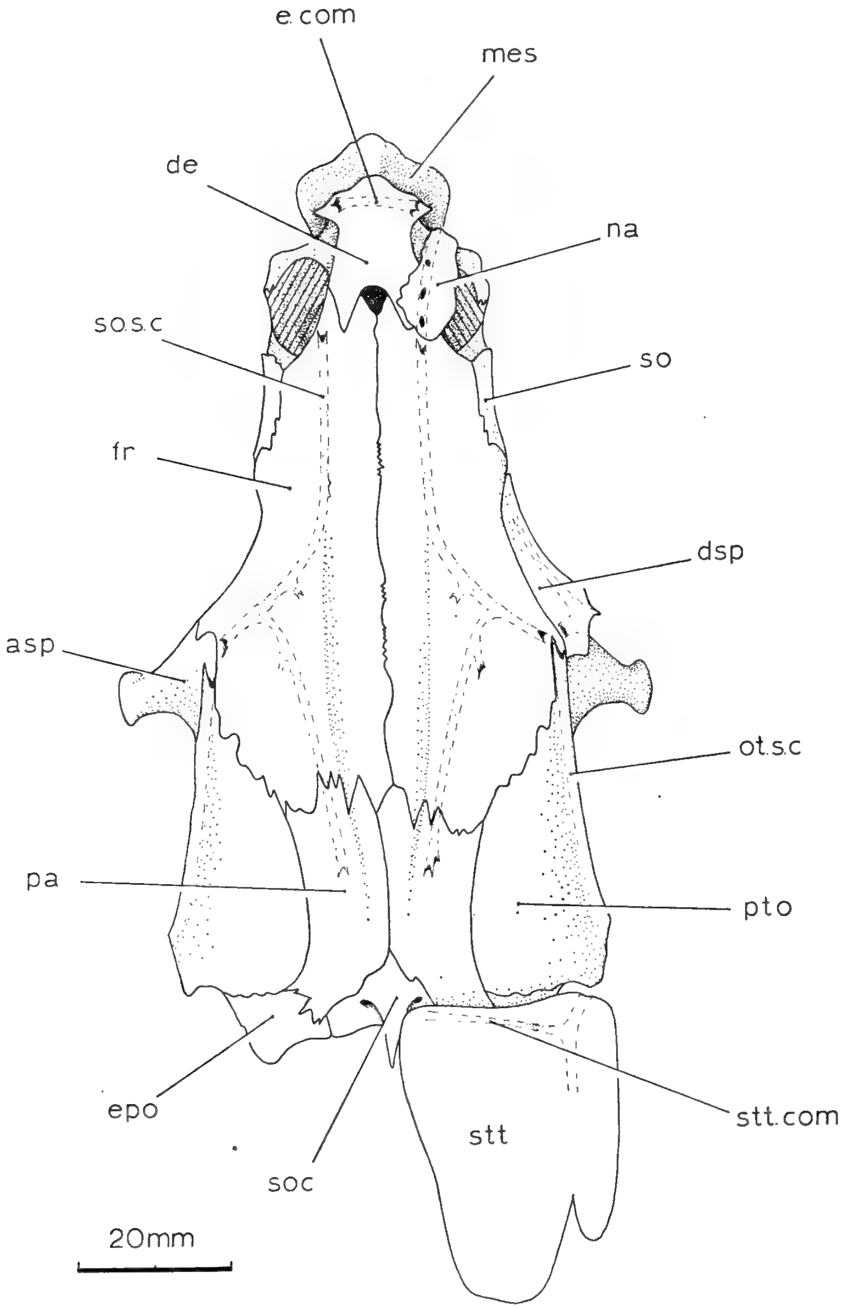

FIG. 20. *Tarpon atlanticus* (Cuvier & Valenciennes). Neurocranium in dorsal view. Nasal, dermosphenotic and supratemporal are shown on the right side only. This and Text-figs. 21–27 are each based on several adult specimens. Hatched areas represent cartilage.

parietal. The surface of the frontal is marked by a very shallow ridge which runs the length of the bone and extends posteriorly on to the parietal.

Anteriorly the supraorbital canal is contained within a horizontal plate-like nasal. In smaller individuals the nasal is tubular, as in *Elops*. Above the orbit the frontal has a narrow rebate for the narrow supraorbital. In larger specimens the supraorbital is tightly bound to the frontal.

The parietal is three times as long as wide and is overlapped by the frontal anteriorly. During growth the shape of the parietal changes from broad to narrow. The pterotic is triangular and its true extent may not be seen in dorsal view, due to the convexity of the skull roof.

Beneath the dermethmoid the ethmoid cartilage extends back to the orbit. Anteriorly, where the cartilage projects beyond the dermethmoid, it becomes ossified as it expands over the dorsal part of the vomer. This ossified mesethmoid is securely attached to the vomer, so that its individuality may only be recognized in young, alizarin-stained specimens. The dorsal surface of the mesethmoid bears a median ridge on either side of which is an ovoid depression. The depression receives the head (cranial condyle) of the maxilla, while the premaxillae meet one another immediately above the median ridge.

The medial wall of the nasal capsule is mainly cartilaginous. The lateral ethmoid is ossified in the lateral part of the planum antorbitale. From its sutural connection with the underside of the frontal the lateral ethmoid curves anteriorly and ventrally to contact the dermethmoid wing. The ventral surface of this contact bears a large cartilaginous meniscus which receives the dorsal surface of the palatine head.

The vomer underlies the mesethmoid and the anterior end of the parasphenoid. In ventral view it is diamond-shaped with the posterior angle produced in an elongated point which interdigitates with the parasphenoid. The dorsal surface of the vomer contributes to the facet receiving the maxillary head. The vomer bears an ovoid patch of numerous fine, backwardly pointed teeth. The confluence of paired vomerine tooth plates is more complete in adult *Tarpon* than in *Elops*.

From the vomer the parasphenoid narrows beneath the orbit before expanding at the level of the ascending wings. Posteriorly the parasphenoid tapers and divides into two prongs which end below the posterior part of the basioccipital. The gap between these two prongs represents the anterior part of a groove beneath the basioccipital and the first vertebral centrum. The dorsal aorta runs in this groove and divides into the lateral dorsal aortae at its anterior end. Such a groove is clearly necessary in this form since the swimbladder diverticulum is pushed tightly against the skull base beneath the basioccipital. Beneath the ascending process the parasphenoid is produced laterally in a small prominence at the apex of which the internal carotid artery enters the myodome. Immediately anterior to this prominence a shallow groove curves antero-ventrally and marks the cranial origin of the adductor arcus palatini musculature. A very narrow band of small granular teeth is found on the parasphenoid beneath the orbit. In all megalopids the parasphenoid tooth patch is less extensive than that of the Elopidae.

The pterotic forms the posterior part of the hyomandibular facet and the dorsal region of the subtemporal fossa. The posterior face of the pterotic forms the roof

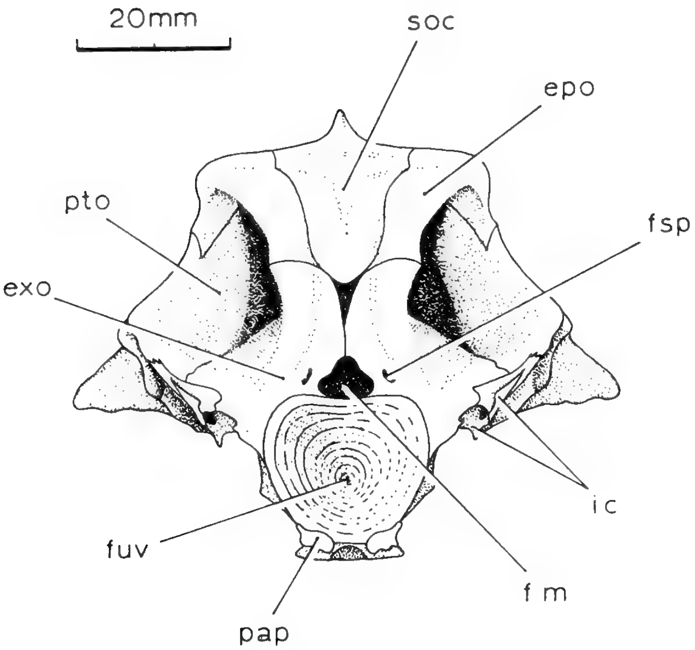

FIG. 21. *Tarpon atlanticus* (Cuvier & Valenciennes). Neurocranium in posterior view.

and lateral border of the post-temporal fossa. The exoccipital is large, forming the ventral border to the post-temporal fossa opening, and the dorsal and lateral margins of the foramen magnum. Along the medial border of the post-temporal fossa the exoccipital forms a ridge which is continued on the epiotic. Medial to this ridge both bones exhibit concave posterior faces. Thus the surface topography of these bones results in there being a median depression flanked on either side by the post-temporal fossae. Beneath the foramen magnum the exoccipital bears a facet which articulates with the first vertebral centrum. On the lateral face of the exoccipital and basioccipital there is a prominent postero-ventrally inclined ridge which provides a point of attachment for the anterior diverticulum of the swimbladder (Greenwood 1970a has described and figured the extension of the swimbladder on the otic region of the skull). Baudelot's ligament inserts on the posterior face of the basioccipital part of the ridge. The exoccipital also contributes to the subtemporal fossa. Beneath the subtemporal fossa the exoccipital exhibits a marked depression. Into the upper part of this depression (which is covered in lateral view by the intercalar, not described here, see Greenwood 1970a) opens the vagus foramen, immediately preceded by the much smaller glossopharygeal foramen. The jugular vein runs along the roof of this depression.

Beneath the exoccipital the basioccipital forms the inner wall of the periotic bulla. The ontogenetic changes that affect the basioccipital are discussed by Greenwood (1970a).

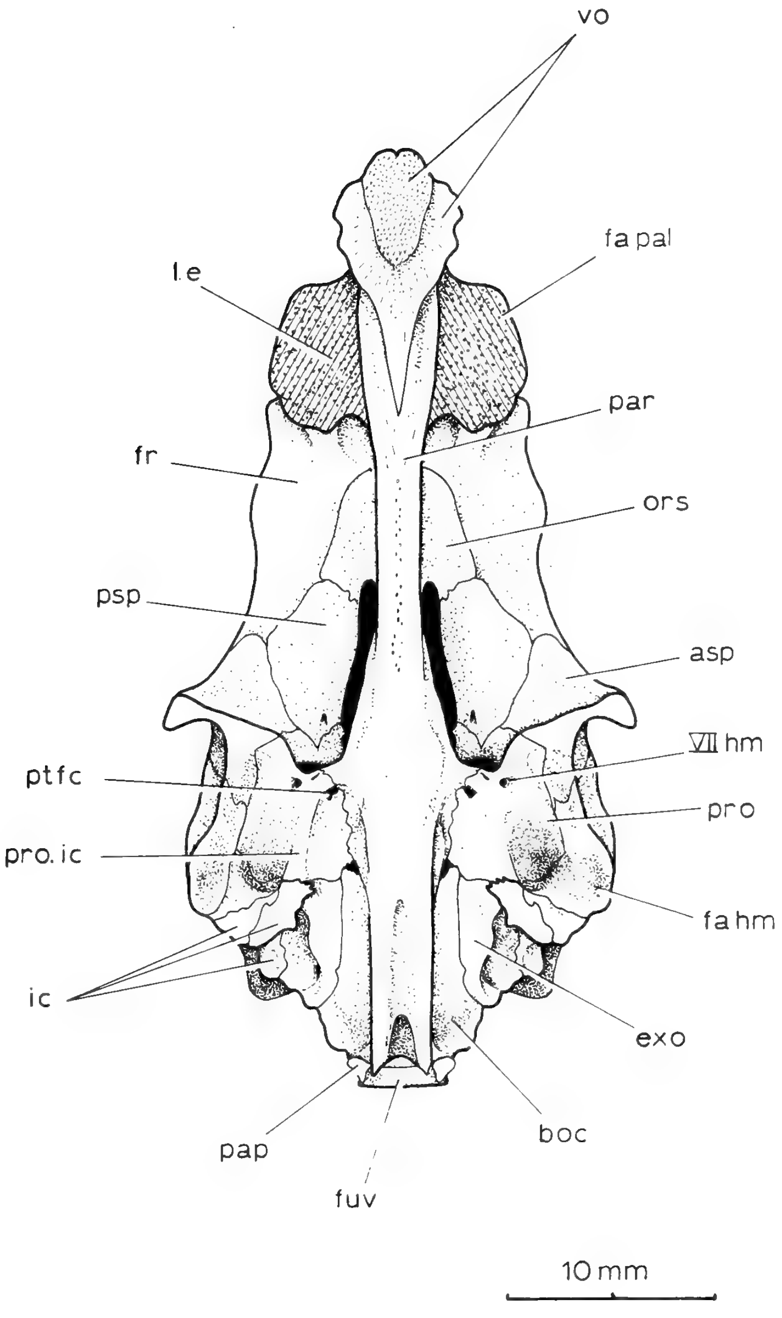

FIG. 22. *Tarpon atlanticus* (Cuvier & Valenciennes). Neurocranium in ventral view. Hatched areas represent cartilage.

The posterior face of the basioccipital and the exoccipital provide a tripartite facet for the first vertebral centrum, which is a functional part of the neurocranium. The centrum bears autogenous parapophyses and a neural arch.

The prootic is, as usual, of complex shape. The lateral face contributes to the hyomandibular facet, the subtemporal fossa and the medial wall of the periotic chamber. A stout ridge runs horizontally across the lateral face of the prootic beneath the subtemporal fossa. The jugular canal opens near the posterior border of the prootic, immediately beneath the horizontal ridge. The hyomandibular foramen is large and points dorsally above the pars jugularis. In some (particularly large) specimens an additional foramen (Text-fig. 23) is situated dorsal to the hyomandibular foramen (Greenwood 1970a : pl. 3, fig. 1). The significance of this foramen is not clear ; it may provide a separate opening for the efferent hyoidean artery. Another foramen of inconsistent occurrence may be seen immediately posterior to the hyomandibular foramen. Greenwood (1970a) identifies this as ' the foramen for the head vein ' but this is unlikely since in the specimen figured (Greenwood 1970a : pl. 3, fig. 1) there is a foramen for the head vein in the usual position and also the foramen in question has no connection, direct or indirect, with the pars jugularis but opens into the post-temporal fossa. Dissection of a specimen showing a foramen in a similar position failed to reveal any function. A palatine branch of the trigeminal nerve leaves the prootic by a slit-like foramen beneath the level of the pars jugularis. The orbital artery pierces the prootic near its suture with the parasphenoid.

The medial wall of the pars jugularis is pierced by two large foramina. The posterior and more ventral of these is the facial foramen while the anterior is the trigeminal foramen (the profundus ciliaris also passes through this foramen). The anterior face of the prootic contacts the autosphenotic and pterosphenoid dorsally and the parasphenoid and basisphenoid ventrally. The anterior face slopes posteroventrally from its dorsal contact with the pterosphenoid. Ventrally the prootic turns horizontally meeting its partner in the mid-line to form the prootic bridge. The abducens nerve pierces the bridge.

The pterosphenoid is inclined almost horizontally. The trochlearis leaves the endocranial cavity through a small foramen in the prootic. It passes into the pterosphenoid to run forward within the bone, leaving the pterosphenoid at its anterior limit. The anterior margin of the orbitosphenoid is notched by the exit of the olfactory tract. The orbitosphenoid forms the anterior wall of the post-temporal fossae.

The median basisphenoid has a stout pedicel which in older specimens becomes firmly attached to the parasphenoid. From the posterior border two posterolaterally inclined prongs enter the posterior myodome cavity. The median basisphenoid pedicel bifurcates dorsally to form two short wings which contact with the prootics.

The post-temporal fossae are enormous. The posterior opening of each fossa is deeper than wide (cf. *Megalops*). The fossae extend right forward to the anterior end of the orbitosphenoid and meet in the mid-line above the endocranial cavity, from which they are separated by cartilage. The increased depth of the

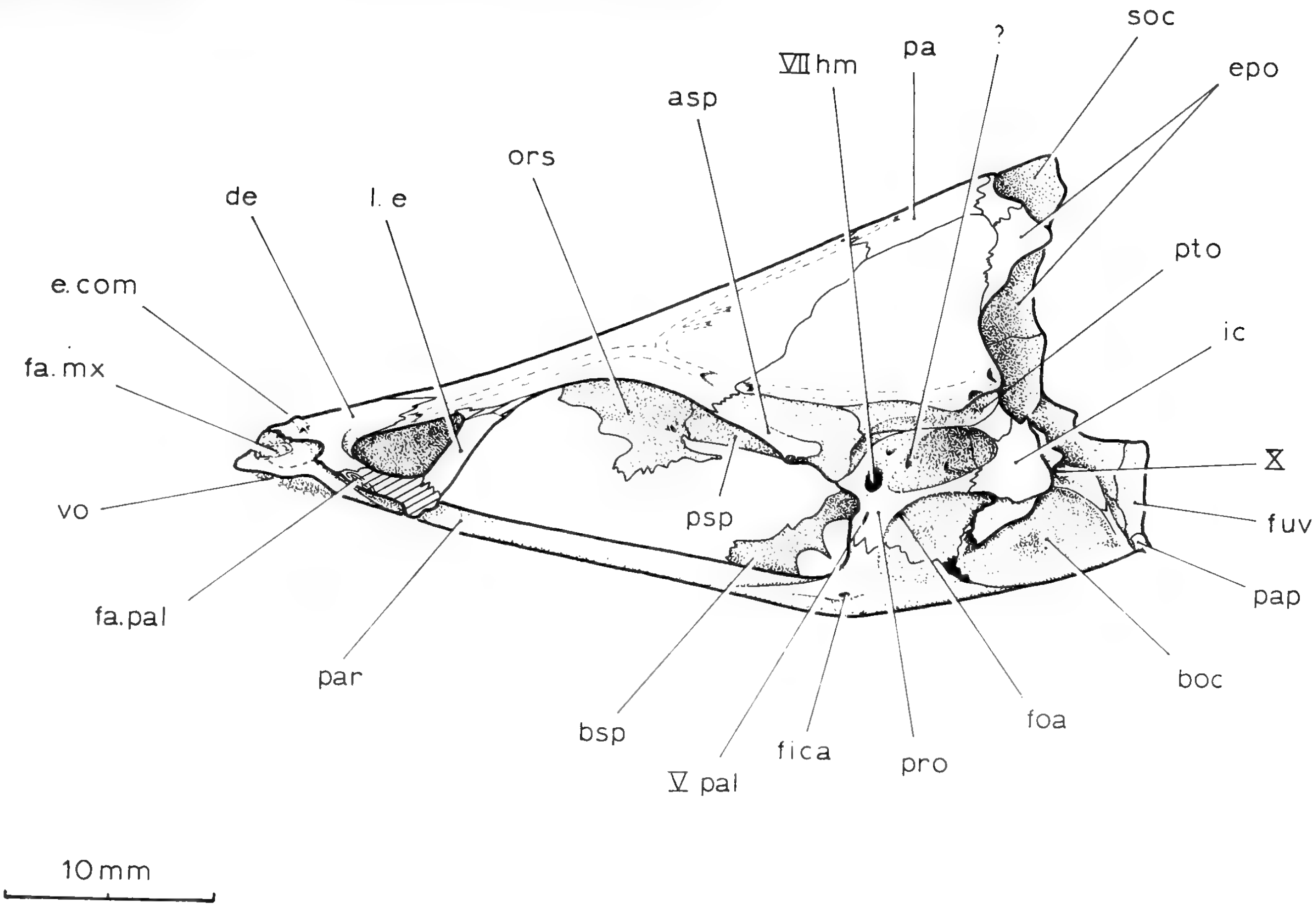

FIG. 23. *Tarpon atlanticus* (Cuvier & Valenciennes). Neurocranium in left lateral view. Hatched areas represent cartilage.

skull at the occiput is due to the dorsal development of these fossae. Epaxial trunk musculature occupies the fossae and is inserted on the walls and on a stout ligament which inserts on the medial surface of the autosphenotic.

Hyopalatine bones. This series is almost as deep as long in adult specimens, but in younger specimens the series is considerably longer than deep. Correlated with this deepening during growth there is a slight forward shift in the quadrate/mandibular articulation. In the adult it lies beneath the posterior half of the orbit.

The hyomandibular is vertical. Its head has anterior and posterior expansions. The external surface of the bone is marked by a prominent ridge which ends dorsally in a small dorso-lateral projection. Immediately behind this ridge there is a groove. The hyomandibular nerve penetrates the medial face immediately beneath the head and divides into an opercular branch and a combined mandibular and hyoidean branch. The former branch leaves the hyomandibular on a level with the opercular process. The latter opens into the posterior groove immediately beneath the opercular process. The anterior border of the hyomandibular is produced into a narrow, very thin wing of bone.

The long symplectic is inclined forwards at about 45° and fits into a deep groove upon the quadrate. The dorsal end of the symplectic overlaps the preoperculum. The quadrate is the usual fan-shaped bone. Ventrally there is an enlarged, transverse condylar surface behind which, in larger specimens, there is a shallow notch. Such a notch may limit the downward movement of the mandible. The anterior border of the quadrate fits into a groove on the ectopterygoid.

The metapterygoid is separated from the dorsal margin of the quadrate by a thin slip of cartilage. Upon the lateral face the metapterygoid is produced postero-dorsally as a thin wing which overlaps the ventral part of the hyomandibular. Between this overlap of the hyomandibular and metapterygoid there is a considerable space, the hyomandibular-metapterygoid cup, into which insert the deeper divisions of the levator arcus palatini muscles.

The endopterygoid is overlapped posteriorly by the metapterygoid. Anteriorly the endopterygoid is ovoid in outline and fits between the posterior region of the auto- and dermopalatine. The ectopterygoid is a boomerang-shaped element, the two limbs being equally developed. The posterior and dorsal margins are grooved to receive the quadrate and endopterygoid.

The dermopalatine is a flat plate of bone partially overlapping both the endo- and ectopterygoid. The medial edge of the dermopalatine lies against the border of the vomerine tooth patch. An autopalatine may ossify in large individuals. Anteriorly the palatine cartilage is expanded into a large knob, the dorso-medial face of which contacts the cartilage underlying the suture between the dermethmoid and lateral ethmoid. The antero-lateral aspect of the knob articulates with the palatine head of the maxilla. Between these two elements lies a small biconcave meniscus of cartilage.

Much of the buccal face of the hyopalatine series bears teeth. Those on the palatine are small, pointed and directed posteriorly. Upon the endopterygoid, ectopterygoid (and, in older specimens, the metapterygoid) the teeth are slightly smaller and more granular in form. In young individuals the teeth are relatively larger,

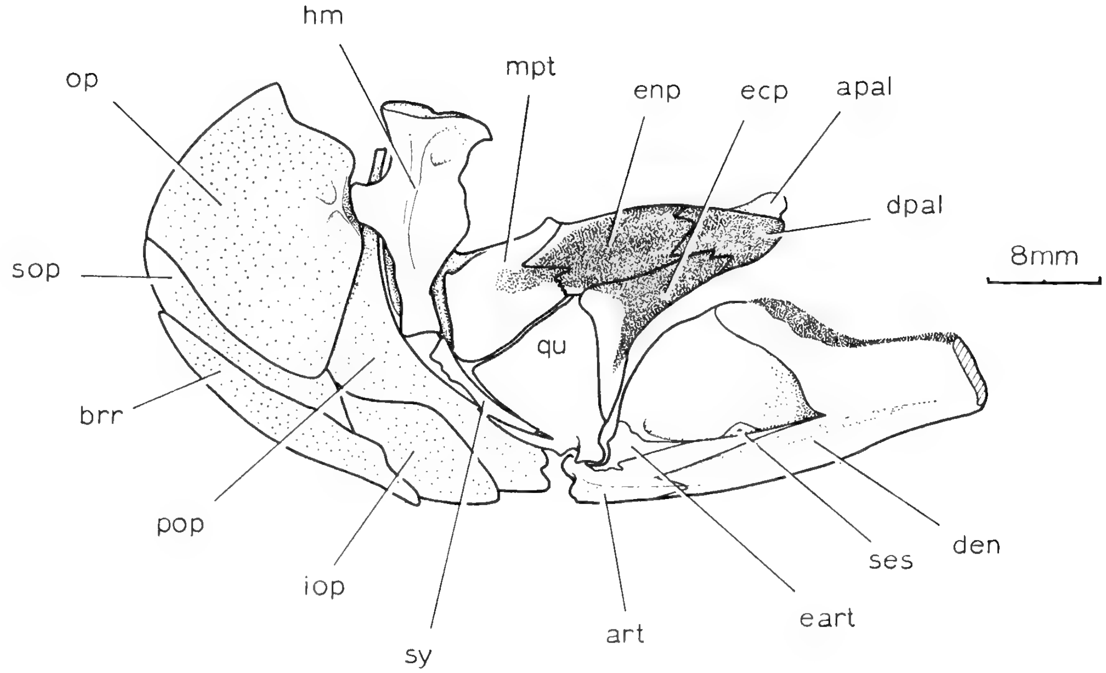

FIG. 24. *Tarpon atlanticus* (Cuvier & Valenciennes). Hyopalatine bones, opercular series, uppermost branchiostegal and mandible of the left side in medial view.

pointed, but much more sparsely distributed. Those on the ectopterygoid are confined to the extreme lateral border.

Dermal upper jaw. The upper jaw ends behind the eye. In young individuals the jaw is relatively narrow with a slightly curved oral margin but in adult specimens the jaw is deeper and the oral margin is markedly rounded.

The premaxilla occupies 20 per cent of the total jaw length. Anteriorly the premaxilla is deep, meeting its partner in the mid-line. The dorsal border is produced posteriorly as a rudimentary articular process which overlaps the maxilla. The oral border of the premaxilla bears many small, pointed teeth.

The maxilla is thin posteriorly but thickens anteriorly as it curves medially to articulate with the ethmoid region by a slightly expanded head. A small palatine process arises from the lateral face of the maxilla, beneath which there is a groove receiving the posterior (dorsal) border of the premaxilla. Two supramaxillae overlap the dorsal margin of the maxilla. The smaller anterior supramaxilla is ovoid while the larger posterior element has a spine passing dorsal to the anterior supramaxilla. A broad band of teeth is borne by the maxilla. The greater width of this tooth band is on the medial side of the bone.

Mandible. Although the total length of the mandible equals that of the upper jaw, the mandible protrudes in front of the premaxilla and the mouth is upwardly directed. The profile of the dentary symphysis continues that of the skull roof in adult specimens, but in young individuals this is not so and the dentary symphysis is relatively shallow.

The dentary forms two-thirds of the mandible. The ventral margin is slightly inflected. Anteriorly the dentary curves markedly inwards to the symphysis. For one third of the mandibular length the oral margin of the dentary is parallel to the ventral border, but behind this level the profile rises steeply to form much of the elongate coronoid process. In young individuals the dentary is relatively shallower and the oral margin is gently curved. Teeth are borne in a broad band along the oral margin of the dentary. The tooth band increases in width posteriorly where it spreads over the medial surface of the bone. Teeth borne by the dentary are similar to those of the upper jaw and dermopalatine. On the medial surface of the dentary there is a deep, anteriorly directed, crescent-shaped fossa which receives the anterior end of the A_w muscle.

The articular forms the posterior part of the coronoid process and the outer portion of the articulatory cup. The medial surface of the articular has a prominent ridge which is continuous with a ridge upon the dentary. The endosteal articular forms the inner portion of the articulatory cup and sends a short process forward on the top of the articular ridge. A small sesamoid articular occurs anterior to the endosteal articular.

Circumorbital series. This series is composed of seven bones, one of which, the supraorbital, is an anamestic component. The antorbital is a narrow strut, inclined antero-ventrally from its loose connection with the supraorbital. Part of the ventral antorbital margin lies against the dorsal border of the lachrymal (the first infraorbital). The latter element is rounded anteriorly. Posteriorly it narrows where it is partially overlapped by the second infraorbital. On the antero-dorsal part of the

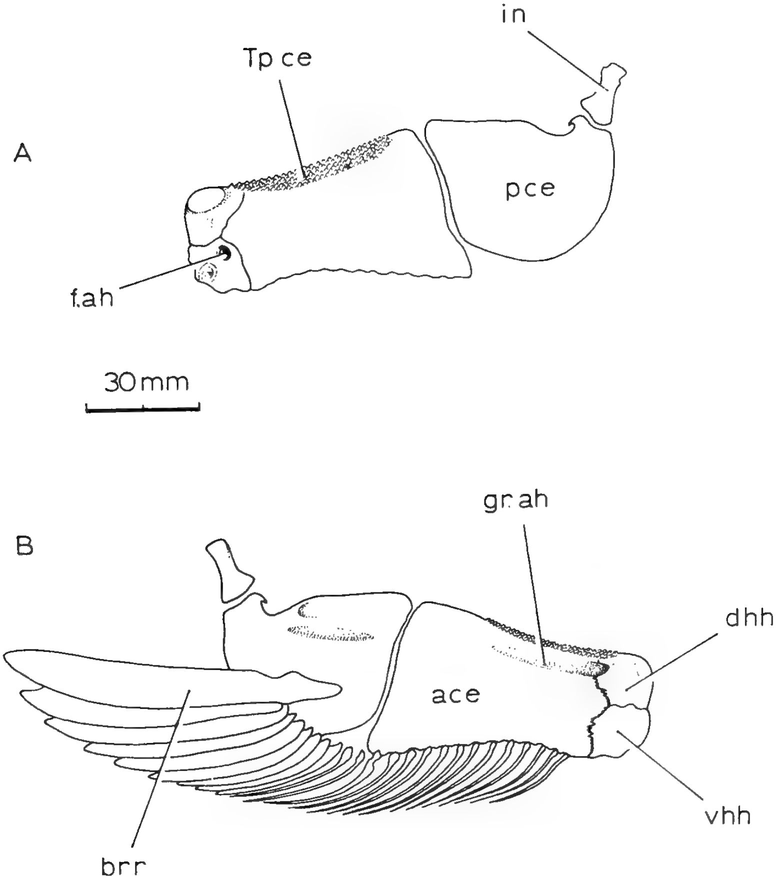

FIG. 25. *Tarpon atlanticus* (Cuvier & Valenciennes). Hyoid bar and branchiostegals (except uppermost ray) of right side in A, medial view and B, lateral view.

first infraorbital there is a prominent knob articulating with the maxilla. Infraorbitals 3, 4 and 5 form a broad, thin bony plate. The dermosphenotic is a narrow bone which tapers as it curves anteriorly to almost touch the supraorbital. It is considerably stouter than any other infraorbital.

Hyoid arch, gill arches and gular plate. The ceratohyal, as usual, comprises anterior and posterior elements which are united by cartilage. A short, stout interhyal is connected to the posterior ceratohyal by cartilage. The upper and lower hypohyals are synchondrally united to one another and to the anterior ceratohyal. The medial surface of the lower hypohyal bears a small ovoid facet to which a ligament from the urohyal is attached. A medial prominence on the upper hypohyal lies against the basihyal. The afferent hyoidean artery pierces the medial surface of the lower hypohyal. From here the artery passes into the upper hypohyal, emerges from its dorsal surface, and runs posteriorly in a groove on the lateral face of the anterior ceratohyal. A foramen on the medial surface of the upper hypohyal connects with the arterial canal: the significance of this foramen is not clear.

A tooth plate is associated with the dorsal margin of the anterior ceratohyal and part of the upper hypohyal. Additional tooth plates are scattered in the skin covering the medial surface of the anterior ceratohyal.

There are 21–24 branchiostegal rays. The anterior 13 are thin and pointed (almost filiform) and attached to the ventral margin of the anterior ceratohyal which is scalloped for their reception. As one passes back along the series the rays become spathiform (terminology after McAllister 1968) and are attached to the lateral surface of the posterior ceratohyal. The upper branchiostegal extends further forward than those preceding it and is more closely associated with the interoperculum.

The gill arch structure is primitive for a teleostean fish. For instance, the basibranchial complex is formed by independent dermal and endochondral elements and the tooth plates associated with the cerato- and epibranchials are very small and numerous.

The basibranchial complex is formed by an ossified basihyal succeeded by three ossified basibranchials. The first basibranchial is short and deep and set slightly below the level of the elongate second and third elements. The fourth basibranchial is represented by cartilage. Tooth plates associated with the basihyal and basibranchial are an elongated basihyal plate succeeded by a long tooth plate overlying the first three basibranchials. The tooth plate overlying the fourth basibranchial varies in shape and size from specimen to specimen: in young adults there are two ovoid tooth patches set one behind the other, but in old specimens only a single plate is recognizable. Thus, throughout life there is some degree of assimilation (Nelson 1969a: 484).

Hypobranchials 1–3 are attached to the posterior edge of their respective basibranchial supports. There are five ceratobranchials and four epibranchials, the fourth epibranchial with a large expansion posteriorly. There is no fifth epibranchial as figured for *Megalops* by Holstvoogd (1965: fig. 3b). Of the four infrapharyngobranchials the anterior three are ossified and the fourth is represented in cartilage. The first infrapharyngobranchial articulates with the parasphenoid. Suprapharyngobranchial 1 is ossified and attached to the dorsal limb of epibranchial 1 by cartilage.

Tooth plates of the first arch are associated with hypo-, cerato-, epi- and infrapharyngobranchials. Gill-rakers are present, associated with all the above elements except the first and fourth infrapharyngobranchials. On the first arch there is a total of 62 gill-rakers (16 on the hypobranchial, 24½ upon the ceratobranchial, 20½ on the epibranchial and 1 lying free between the epibranchial and infrapharyngobranchial). Immediately behind the gill-rakers and resting upon a ledge near their base there is a single row of rectangular tooth plates. On the ceratobranchial and much of the epibranchial there is a one-to-one correspondence between tooth plate and gill-raker. At the top of the epibranchial the tooth plate row breaks into smaller irregular plates which continue in the dermis overlying the infrapharyngobranchial. Over the hypobranchial the tooth plate row has consolidated into larger

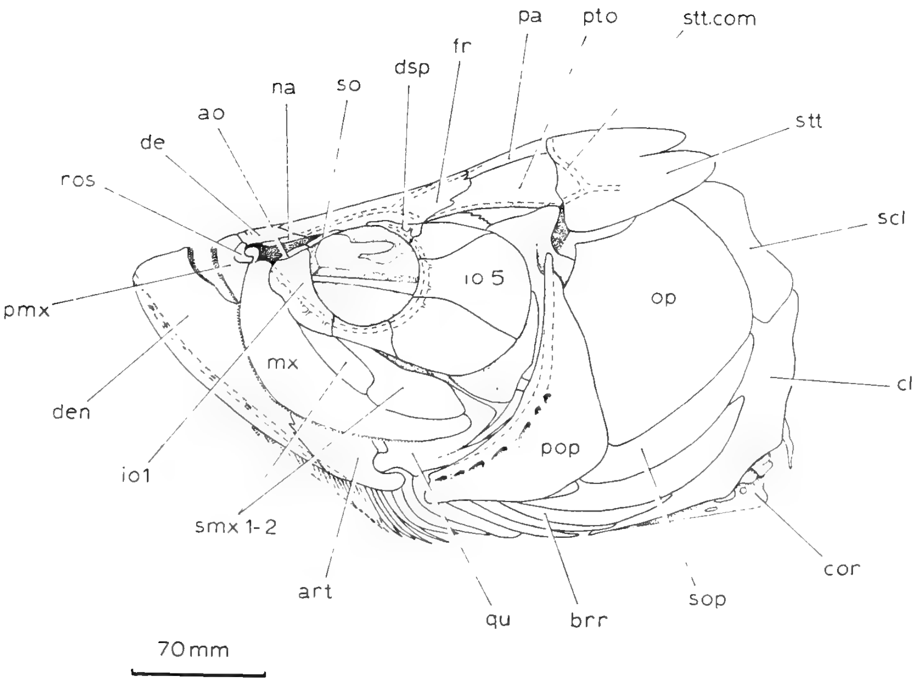

FIG. 26. *Tarpon atlanticus* (Cuvier & Valenciennes). Cranium in left lateral view.

units. The posterior face of the hypo-, cerato- and epibranchial is covered by two rows of tooth plates. The more dorsal of these is formed by very small plates, irregular in shape and not always set in a linear fashion (indeed this ' row ' is best described as a band of plates). The ventral row is more easily definable with the tooth plates larger and regular in shape and set in a definite row. At the dorsal end of the epibranchial the upper row of tooth plates becomes a broad band which runs in continuity with the ventral row.

The tooth plates associated with the second and third arches are set in similar fashion to those of the first. The tooth plates associated with the second infrapharyngobranchial are larger than those on the first. The third infrapharyngobranchial bears a well-developed tooth plate which lies in series with that associated with infrapharyngobranchial 4.

The tooth plates upon the fourth arch are similarly distributed to those on the first three, but the most posterior row is formed by plates resembling reduced gill-rakers and these interdigitate with the reduced gill-rakers upon the fifth ceratobranchial. The three tooth-plate rows may still be recognized on the fifth ceratobranchials but the plates of the posterior row have become much enlarged and together form the lower pharyngeals.

The urohyal extends posteriorly to the level of the fourth basibranchial. Anteriorly it is attached to the lower hypohyal of either side by a short ligament. The gular plate is large, extending for at least half the length of the mandible.

Opercular series. The greatest width of the operculum occurs at the level of the articulation with the hyomandibular. Above the articulation the anterior margin of the operculum is concave. The posterior border of the bone is smoothly rounded. Postero-ventrally the ventral margin is obliquely inclined. The suboperculum is essentially a parallel-sided bone with rounded anterior and posterior margins. The interoperculum is large and rhomboidal in shape. It is attached to the articular by a stout ligament.

The preoperculum has a smoothly concave anterior border. Mid-way along its length there is a small prominence anteriorly for the insertion of part of the adductor mandibulae muscle. The preoperculum is expanded postero-ventrally.

Cephalic sensory canal system. The supraorbital canal penetrates the frontal above the autosphenotic spine and curves anteriorly to run within the shallow ridge. A large backwardly directed branch of the canal runs within the posterior part of the ridge to open on to the parietal. Within the frontal the main secondary branches of the canal are as illustrated (Text-fig. 20) but in younger individuals the branches are far more numerous.

A large otic sensory canal runs along the lateral border of the pterotic opening anteriorly above the autosphenotic spine and posteriorly above the posterior limit of the hyomandibular facet.

The infraorbital sensory canal runs near to the orbital margin of all infraorbitals except the first where it passes diagonally across the bone to open at the base of the antorbital. Short branches are given off posteriorly from the main canal. Within the skin these canals extend for a considerable distance and exhibit prolific branching. The infraorbital canal bifurcates as it leaves the anterior (dorsal) end of infraorbital 1, sending a thin antorbital branch (adnasal branch of some authors, e.g. Nybelin 1967a) backwards, and a larger canal forwards which runs through a rostral ossicle before uniting with the ethmoid commissure (this region of the canal system has been excellently described and figured by Nybelin 1967a). The infraorbital canal meets the supraorbital and otic canals within the skin above the dermosphenotic.

The preopercular sensory canal runs very close to the anterior border and opens on to the surface of the bone through four to seven pores.

The mandibular sensory canal pierces the posterior surface of the articular and runs within this bone and the dentary. The canal opens to the surface by pores which become more numerous anteriorly.

Pectoral girdle and fin. The supratemporal is very similar to that of *Elops hawaiensis* (p. 22). The pattern of the contained lateral line and supratemporal commissure is also similar to *Elops*, with the difference that the commissure in *Tarpon* has very few pores.

The post-temporal is a large concavo-convex bone disposed in the vertical plane. The anterior margin shows three projections, separated by two shallow indentations. The medial (dorsal) projection overlies the dorso-lateral face of the epiotic process to which it is attached by a ligament. The middle process is wide and truncated anteriorly. To this limb is attached a stout ligament which runs into the post-temporal fossa. The spine-like lateral (central) process is inclined antero-ventrally and connects with the basal part of the intercalar by a stout ligament.

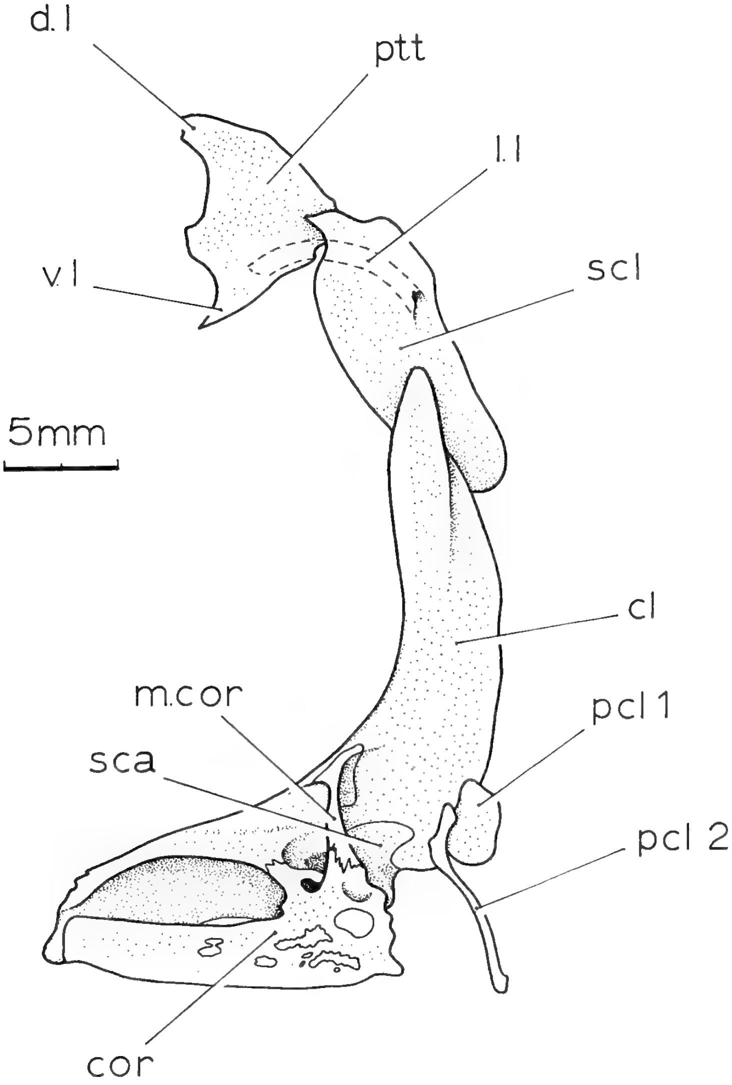

FIG. 27. *Tarpon atlanticus* (Cuvier & Valenciennes). Pectoral girdle of right side in medial view.

The lateral line canal descends from the underside of the supratemporal and runs within a bony tube on the outer surface of the post-temporal before leaving the bone to pass into the supracleithrum. Posteriorly the post-temporal has a small prominence which fits into a depression at the dorsal end of the supracleithrum.

The blade-shaped supracleithrum is pierced dorsally by the lateral line canal which runs obliquely across its lateral face. Numerous ventral branches are given off from the supracleithral canal.

The cleithrum is large and curves antero-ventrally. The anterior tip meets its fellow in the mid-line. The anterior margin of the bone is thickened and dorsally this thickening forms a short spine to which Baudelot's ligament is attached. A horizontal ledge projects medially from the ventral part of the cleithrum.

The endoskeletal girdle consists of the scapula, coracoid and mesocoracoid. The scapula is of complex shape. Laterally it spreads over the medial face of the cleithrum. Medially, the horizontal portion of the scapula contacts the coracoid and mesocoracoid through synchondral unions. The posterior margin of the scapula bears a saddle-shaped depression receiving the first pectoral fin-ray. The scapular foramen is incomplete.

The coracoid is elongate and lies in the vertical plane. Posteriorly the lateral face unites with the scapula through a simple synchondral join, and with the mesocoracoid through an interdigitating synchondral join. The coracoid also exhibits a syndesmotic union with the horizontal cleithral ledge. The posterior margin of the coracoid is capped by cartilage. The medial face of the coracoid lies against that of its partner while the anterior margin is bound by loose connective tissue to the cleithrum. A large foramen pierces the coracoid below its union with the scapula and mesocoracoid. The latter bone spreads over the inner surface of the cleithrum. A narrow mesocoracoid arch passes ventro-medially to contact the scapula and coracoid.

There are four ossified radials. The outermost is the shortest and the only member of the series attached to the scapula. The other members of the radial series are attached to the coracoid, the innermost being the longest. There are two postcleithra. The dorsal one is rounded and scale-like. Anteriorly this element bears a small prominence which lies medial to the cleithrum. The ventral postcleithrum is an elongated curved roof. The upper end is somewhat flattened and lies against the medial edge of the dorsal postcleithrum.

There are 14 pectoral fin-rays, the outermost unbranched. All rays are segmented. At the base of the upper half of the first fin-ray there is a triangular splint bone.

Vertebral column. There are approximately 54 vertebrae (range 53–57) of which about 20 are caudal. All centra are amphicoelous and pierced by the notochord.

Most of the centra are isodiametric but those anteriorly are deeper than long. Each centrum is marked laterally by numerous grooves separated by fine ridges, some of which anastomose. The neural arches are autogenous. Each centrum bears pits dorsally for their reception. The neural arches associated with the first 29 centra are expanded distally. Neural spines borne by these arches are slender, straight and remain separate from their fellows of the opposite side. The vertebral centrum which is incorporated into the neurocranium bears a neural arch somewhat broader than those immediately behind, but the neural spine is considerably shorter. The neural spines of the posterior abdominal and caudal region are stout and fused to their partners of the opposite side. The neural arches which support caudal fin-rays are modified for this function and are not considered here (see Hollister 1936).

All of the caudal centra have stout haemal arches and spines. The posterior haemal spines are modified in support of the caudal fin-rays. Autogenous

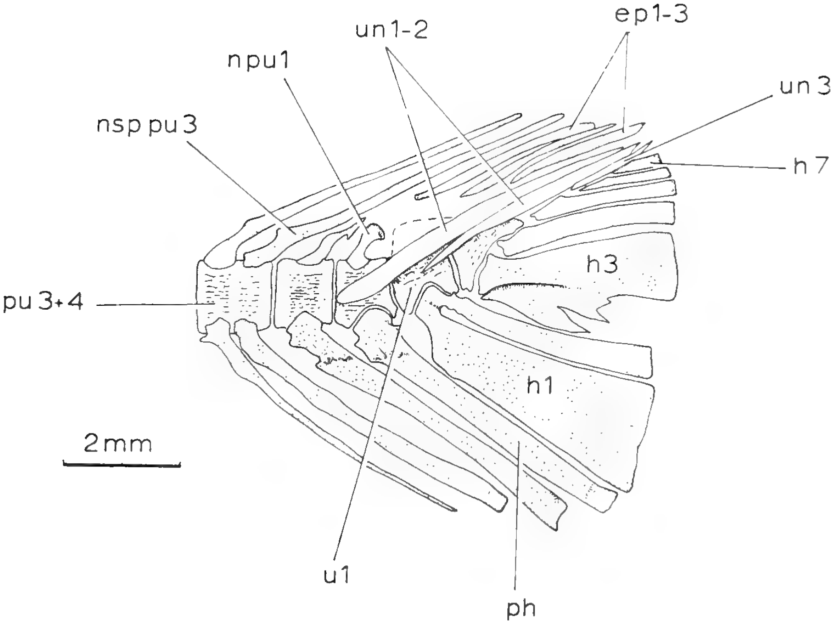

FIG. 28. *Tarpon atlanticus* (Cuvier & Valenciennes). Caudal skeleton in left lateral view. Based on a young individual 87 mm S.L.

parapophyses are found throughout the abdominal region. Those upon the last eight abdominal centra become progressively longer. Pleural ribs are attached to the ventro-posterior aspect of all parapophyses, including those associated with the neurocranial centrum.

Epineurals are attached to the bases of the neural arches throughout the abdominal region. In the caudal region the dorsal series of intermuscular bones have forked bases which are attached to the bases of the neural arches. Epipleural (ventral) intermuscular bones attach to the dorsal surface of the parapophyses. In the caudal region ventral intermusculars are attached to the bases of the haemal arches by tough connective tissue. The ventral intermuscular bones of the anterior 12 vertebrae are attached to the lateral face of the centrum and there are small projections upon the centra to receive the intermuscular heads. Thus in the extreme anterior region the intermusculars are epicentral in position. An intermuscular bone which is attached to the exoccipital appears to lie in series with these epicentrally placed intermusculars. In the caudal region fine intermuscular bones are attached to the centre of each centrum by a narrow strand of connective tissue and are therefore to be regarded as epicentrals. Thus there are three series of intermusculars in the caudal region ; dorsal, epicentral and ventral intermusculars.

Between the neural spines of the first 22 vertebrae there is a series of 23 supraneurals. All but the first are slender and tubular. The first is solid, very broad, particularly in its dorsal extent, and situated anterior to the reduced neural spine associated with the neurocranial centrum. As in *Elops* (p. 25) there is an overlapping of the supraneural and pterygiophore series.

Median fins. The dorsal fin is situated in the centre of the back and is composed of 15 (13–15) fin-rays, of which the first two are unsegmented. The sixth ray is the first branched. Behind the sixth the rays decrease in length except the last, the posterior half of which is produced into a long filamentous structure (see p. 201). The lepidotrichs are supported by 12 pterygiophores, each composed of proximal, middle and distal radials. The first pterygiophore is considerably stouter than those succeeding it, and proximally it extends between the tips of the neural arches of the twenty-first and twenty-second vertebrae.

The origin of the anal fin lies nearer to the pelvic than to the caudal peduncle. The fin is composed of approximately 24 rays (range 22–25), of which the first four are unsegmented. The eighth is both the longest and the first branched ray. The posterior rays increase in length. The posterior half of the last ray may be produced as a short filament (in alcohol-preserved specimens the tips of the fin-rays are often broken). The fin-rays are supported upon approximately 21 pterygiophores. The first, which supports four rays, extends antero-dorsally to end immediately beneath the thirty-first centrum.

The caudal fin has been described and figured by Hollister (1936).

Squamation. The structure of the scales has been dealt with by Hollister (1939) and Cockerell (1912). Consequently only brief mention of them is made here.

There are 41–48 lateral line scales (in specimens examined the mode was 44). The transverse count in front of the dorsal fin is 5/6. Scales of the lateral line are rounded, the transverse and horizontal axes being equal. The anterior border shows three scallops delimited by four radii which extend to the centrally placed nucleus. The tube containing the lateral line has secondary branches, which do not anastomose (cf. *Megalops*).

The general body squamation shows a variation in the scale shape. Those scales immediately behind the cleithrum are deeper than long ; those upon either side of the dorsal mid-line are decidedly longer than deep while those on the caudal peduncle are only slightly longer than deep. The scales which sheath the base of the anal fin (there are no sheathing scales on the dorsal fin, cf. *Elops*) are smaller than other body scales and are ovoid to irregular in shape.

Despite differences in shape the scale ornamentation remains constant. The embedded portion of the scale is marked by concentric circuli composed of many partially fused tubercles. In the exposed portion the circuli break up to an irregular pattern of tubercles. The posterior margin of the scale is very thin, unmarked by circuli or tubercles. Instead the border is finely crenulated. In large scales (i.e. those of large individuals) the posterior scale margin is frequently frayed.

An exception to the above scale types is the scale at the axis of the pelvic and pectoral fins. The axillary scale is elongate, two and a half times as long as deep, rounded anteriorly, pointed posteriorly. The scale is attached to the body wall by a thick flap of skin which inserts on the medial face of the posterior half of the scale. Circuli are absent and the radii, which originate from the anteriorly placed nucleus,

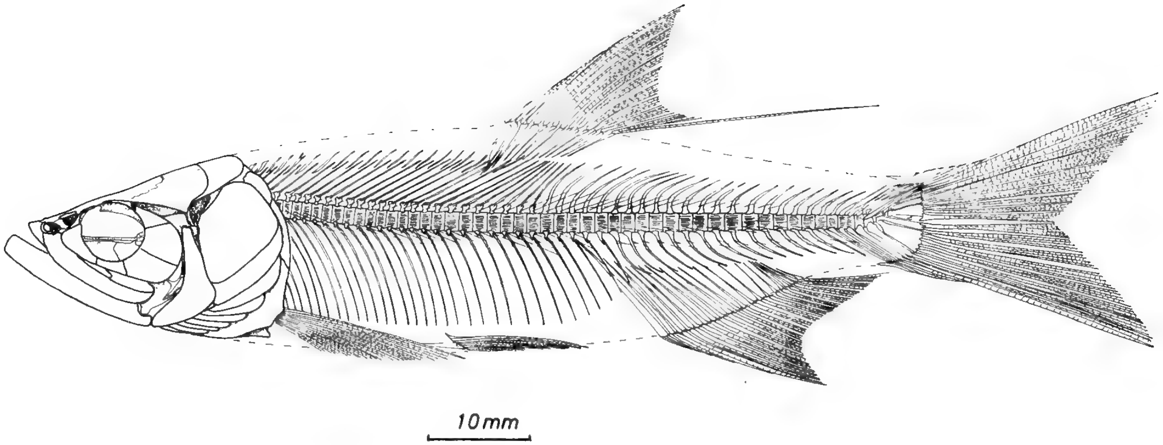

FIG. 29. *Tarpon atlanticus* (Cuvier & Valenciennes). Entire skeleton, scales omitted. Based on a young individual 87 mm S.L.

are irregular in shape. The thinness of the scale, plus the lack of ornamentation (circuli), imparts a flexibility to this structure. All scales show bone cells in the embedded portion.

Genus ***MEGALOPS*** Lacépède, 1803

Diagnosis (emended). Megalopid fishes reaching 1100 mm in length. Neurocranial roof markedly convex above the cranial vault. Parietals as broad as long. Dilatator fossa broad, shallow and without a roof. Process of intercalar forming the lateral wall of the periotic bulla. Jugular canal opening posteriorly into the subtemporal fossa. Maximum depth of the neurocranium occurring at the autosphenotic level. Maxilla not extending behind the eye. Scales with more than five anterior (basal) radii.

Type and only species. *Clupea cyprinoides* Broussonet.

Megalops cyprinoides (Broussonet)

(Text-figs. 30–34)

Diagnosis (emended). *Megalops* in which the origin of the pelvic fin lies beneath that of the dorsal. Maximum depth of body equal to or greater than the head length. Dorsal fin with 17–20 rays, anal 24–27 rays. Vertebral column with 67–68 vertebrae of which approximately 30 are caudal. Lateral line with 36–41 scales. Caudal fringing fulcra 1–9 in number.

Habitat. Coastal fishes, sometimes entering freshwater. Indo-Pacific, between 40° N and 40° S. Longitude extremes, east coast of Africa to Society Islands.

Remarks. *Megalops cyprinoides* has often been cited in the literature. The following works are considered to be the most important anatomical studies : general cranial anatomy, Ridewood (1904) ; intercalar, with respect to the otophysic connection, Greenwood (1970a) ; branchial arches and associated musculature, Holtsvoogd (1965) ; ligaments and musculature concerned with the feeding and gill ventilation movements, Vrba (1968) ; otophysic connection, de Beaufort (1909) ; caudal anatomy, Regan (1910) and Hollister (1939).

The above literature, plus the preceding description of the closely related *Tarpon atlanticus*, renders an osteological description unnecessary. It remains to point out the various differences between the two Recent forms.

The proportions of the skull roof above the otic region of the skull differ from those in *Tarpon*. Thus in *Megalops* the width at the occiput is relatively greater and the distance from the base of the supraoccipital crest to a line drawn between the autosphenotic spines is considerably less than half the length of that line. In *Tarpon* this latter ratio is considerably greater than half, and thus the length of the otic region in *Tarpon* is greater.

The parietals are as broad as they are long and show smooth margins. They are thus like the parietals of young *Tarpon* but unlike the adult *Tarpon* condition, where these bones are approximately three times as long as broad and exhibit zig-zag sutures anteriorly and posteriorly.

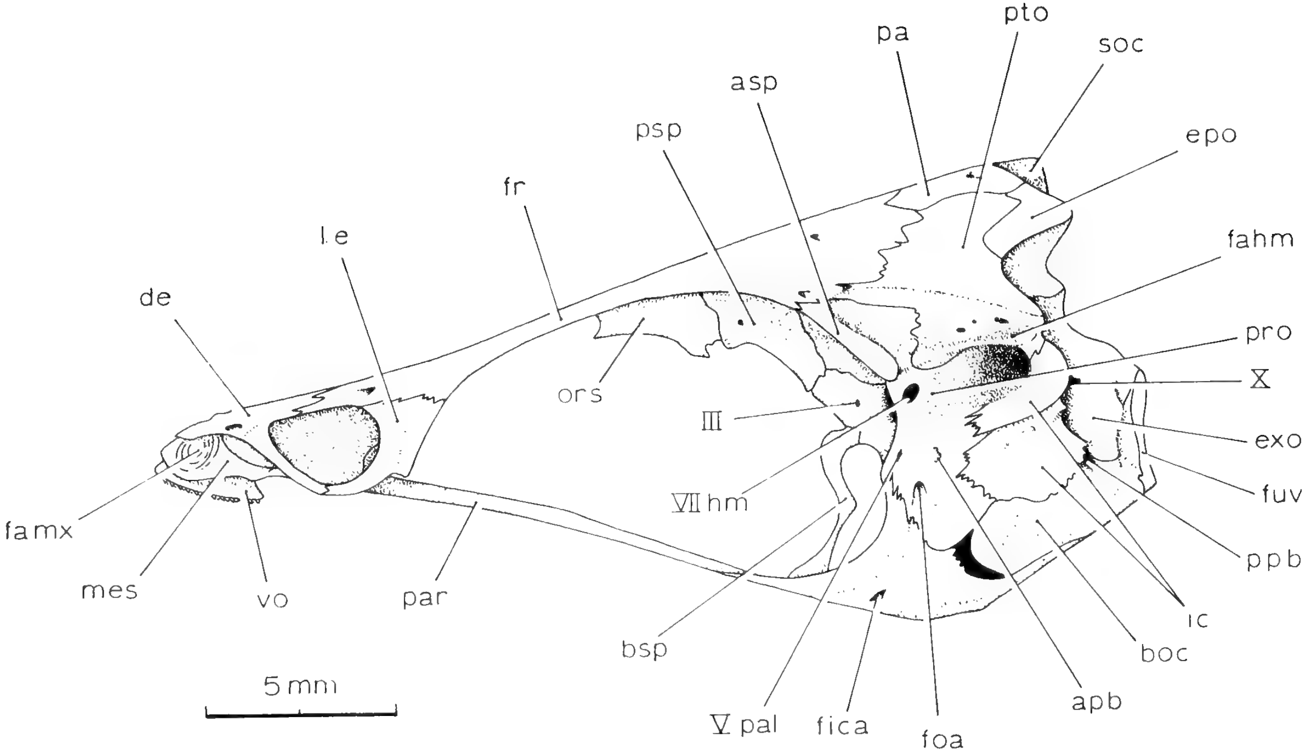

FIG. 30. *Megalops cyprinoides* (Broussonet). Neurocranium in left lateral view. Based on a specimen from Japan, 135 mm S.L.

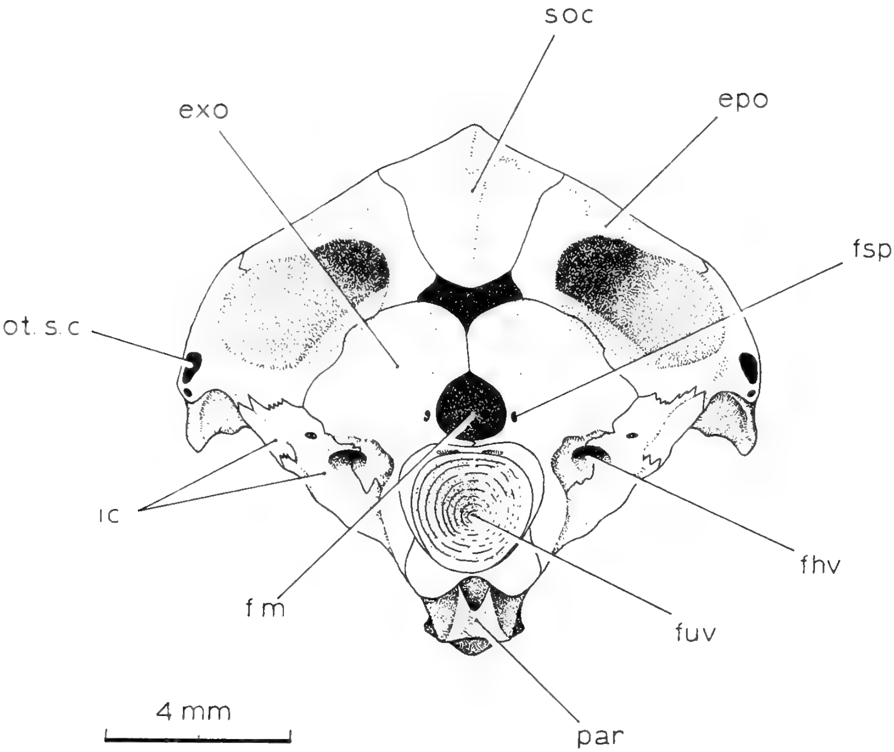

FIG. 31. *Megalops cyprinoides* (Broussonet). Neurocranium in posterior view. Based on same specimen as Text-fig. 30.

The neurocranium of *Megalops* is relatively deeper and the maximum depth occurs at the sphenotic level, whereas in *Tarpon* the maximum depth is at the occiput. The depth of the *Megalops* neurocranium is due to the depth of the prootic bone and parasphenoid ascending wings which in turn may be related to the invasion of the skull by the swimbladder in the following manner. *Megalops* has a large eye, relatively larger than that in *Tarpon*, and thus might be expected to have a large posterior myodome. The extreme anterior end of the swimbladder diverticulum is received in a deep pit within the prootic bone immediately above the prootic bridge, which is, in consequence, displaced ventrally. This lowering of the myodome roof would restrict its volume. Hence it is suggested that the myodome volume is maintained by effectively lowering its floor, i.e. by deepening the prootic and parasphenoid walls. Correlated with this deepening is the angled parasphenoid which is in contrast to the relatively straight bone seen in *Tarpon*.

The intercalar bone of *Megalops* has been well described by Greenwood (1970a), who recognized three interconnected portions ; a basal portion, a lateral shield-like part and a saddle-like wing. The lateral shield-like portion forms a complete bony outer wall to the periotic bulla and is joined to the prootic, basioccipital and exoccipital by a syndesmotic union. The anterior swimbladder diverticulum occupies all of the periotic bulla, leaving no space for the posterior passage of the jugular vein. The jugular vein has therefore to take a different course from that seen in most elopiforms. The vein leaves the pars jugularis above the level of the prootic-intercalar bridge and runs for a short distance along the floor of the subtemporal fossa before passing postero-ventrally through a foramen which represents the space left between the prootic-intercalar bridge and the exoccipital (cf. a similar foramen in *Elops*, p. 12), and leaves the cranium by a foramen between the intercalar and the exoccipital (Greenwood 1970a: pl. 2, *ophv*). This condition is rather different from that seen in *Tarpon* which has been described above. The position of the jugular vein opening in the prootic of *Tarpon* is primitive. Posteriorly, the jugular vein of *Tarpon* has a slightly different relationship to the intercalar. The jugular vein runs back in a groove which is entirely surrounded by the intercalar, there being no contribution by the exoccipital. In short, the jugular vein leaves the cranium of *Megalops* between the exoccipital and the shield-like expansion of the intercalar, whereas in *Tarpon* its exit is surrounded by the basal, crescentic and shield-like parts of the intercalar.

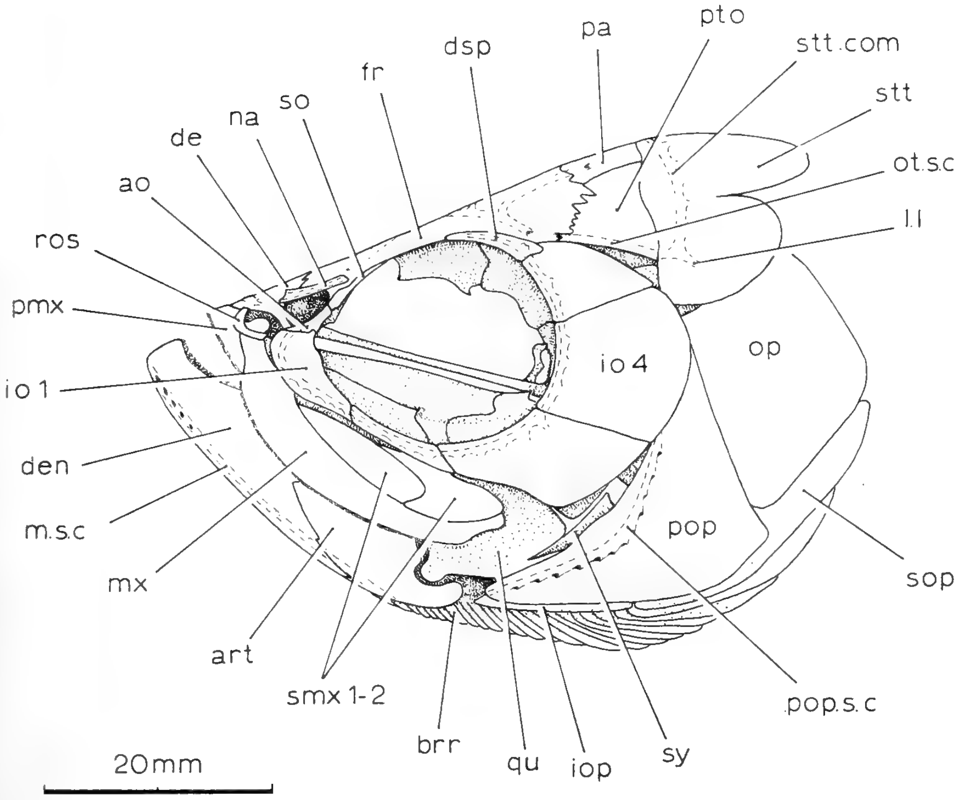

FIG. 32. *Megalops cyprinoides* (Broussonet). Cranium in left lateral view. Based on B.M.N.H. 1876.3.11.1.

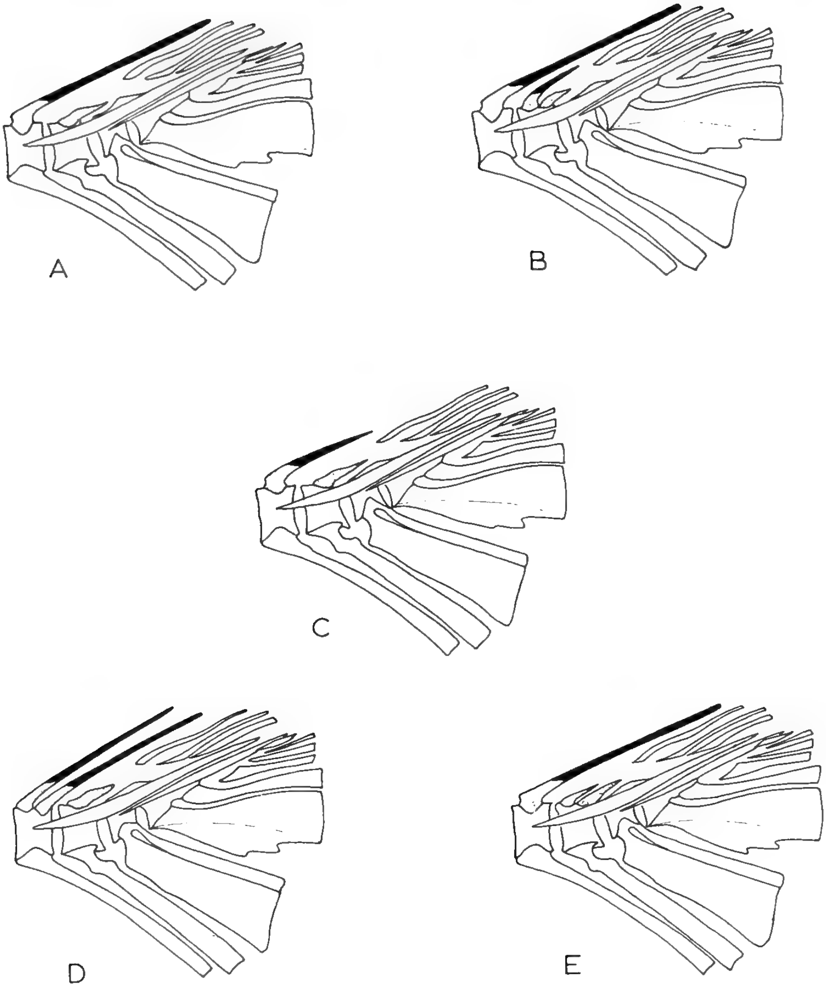

FIG. 33. *Megalops cyprinoides* (Broussonet). Diagram to illustrate variations in caudal osteology. Neural arches stippled, neural spines black.

The only other significant cranial difference between the two genera concerns the length of the maxilla. The maxilla of *Tarpon* extends well behind the level of the eye. That of *Megalops* nearly always terminates at a level beneath the posterior eye border. In two specimens out of a total of 24 examined (ranging in S.L. from 48 mm to 365 mm) the maxilla protruded very slightly beyond the posterior orbital margin.

In the postcranial skeleton *Megalops* differs from *Tarpon* in certain respects which are mentioned in the respective diagnoses. Primarily they concern the position of the ventral fins, the ray counts of dorsal and anal fins and the vertebral and lateral line scale counts.

Hollister (1939) added further differences in the morphology of the lateral line scales and these views are endorsed by the present author. However the differences in the caudal anatomy mentioned by Hollister (1939) are not so consistent as that author implied. For instance, Hollister found a caudal fin-ray count of 34–35 in *Megalops* while that in *Tarpon* never exceeded 32. Such a difference does not seem apparent in the specimens examined here. Hollister (1939) also stated that the basal tip of the first uroneural extended to the anterior part of the second preural centrum in *Megalops* whereas that of *Tarpon* never extended beyond the first preural centrum, a view endorsed by Greenwood (1970a). While this is true of smaller individuals, some large individuals of *Tarpon* exhibit the same uroneural structure as in *Megalops.*

The variability of the neural arches and spines associated with the first two preural centra of *M. cyprinoides* has been noted by Greenwood (1970a). To these variations may be added two more conditions, the range of such structural variation being summed up in Text-fig. 33. The neural arch structure of *Tarpon* is more constant

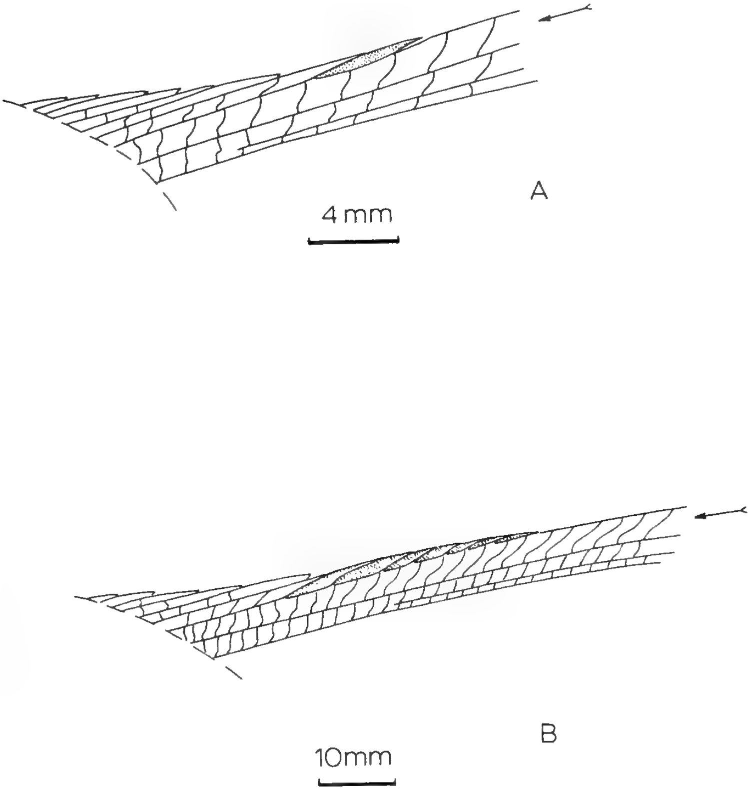

FIG. 34. *Megalops cyprinoides* (Broussonet). Diagram to illustrate fringing fulcra (stippled) preceding the uppermost principal ray (arrowed). A, a young individual B.M.N.H. 1890.2.26.187; B, an old individual B.M.N.H. 1913.4.7.1. Broken line indicates the limit of the body squamation.

(Greenwood 1970a) ; the only variation is the occasional double nature of the second preural vertebra.

One of the characteristic, albeit retentional, features of the Megalopidae is the presence of fringing fulcra on the dorsal surface of the upper principal caudal fin-ray. Regan (1910) noted these in both *Megalops* and *Tarpon*. In both genera fringing fulcra are a very late development ; in *Tarpon* fringing fulcra are not apparent before the fish has reached 170 mm S.L. whereas in *Megalops* (which is a much smaller species) fringing fulcra do not appear before 116 mm S.L. *Tarpon* never shows more than four fulcra (Regan 1910) and generally only one such element is present. *Megalops*, on the other hand, shows a prolific development of about eight in the largest individuals. The fringing fulcra of *Tarpon* are long and slender, the anterior fulcrum (generally the only one) being overlapped to a considerable extent by the posterior dorsal accessory ray. Those of *Megalops* are short, relatively broad and are but little overlapped by the preceding ray so that in many specimens examined the fulcra are not easily distinguished from the terminal segments of the accessory ray. The fringing fulcra are discussed further elsewhere (p. 199).

Genus ***PROTARPON*** *gen. nov.*

DIAGNOSIS. Megalopid fishes in which the neurocranial roof is flat, marked by prominent ridges. Parietals slightly longer than broad. Dilatator fossa narrow, deep and roofed by pterotic and autosphenotic. Posterior opening of the jugular canal below the level of the subtemporal fossa. Maximum depth of the neurocranium at the occiput. Maxilla extending behind the eye. Operculum without antero-dorsal indentation. Dentary shallow anteriorly.

TYPE-SPECIES. *Megalops priscus* Woodward, 1901.

Protarpon priscus (Woodward)

(Text-figs. 35–38)

1844 *Hypsodon toliapicus* Agassiz : **5**, pt. 1 : 101 (*nom. nud.*).
1844 *Megalops priscus* Agassiz : **5**, pt. 2 : 114 (*nom. nud.*).
1845 *Megalops priscus* Agassiz ; Agassiz : 308 (*nom. nud.*).
1854 *Megalops priscus* Agassiz ; Owen : 172 (*nom. nud.*).
1901 *Megalops priscus* Woodward : 24, pl. 3 figs. 3–6.
1966 *Megalops priscus* Woodward ; Casier : 118.

DIAGNOSIS. See Woodward (1901 : 24).

HOLOTYPE. B.M.N.H. 36070, head with opercular apparatus, the skull roof crushed laterally.

MATERIAL. The holotype and paratypes B.M.N.H. P.356, P.637, P.4154a, P.26694 (formerly P.1698) and P.26743. With the exception of the holotype and P.26743 these specimens consist of the posterior half of the neurocranium in varying states of preservation. The only specimens which can be definitely assigned to *P. priscus* are those with cranial remains.

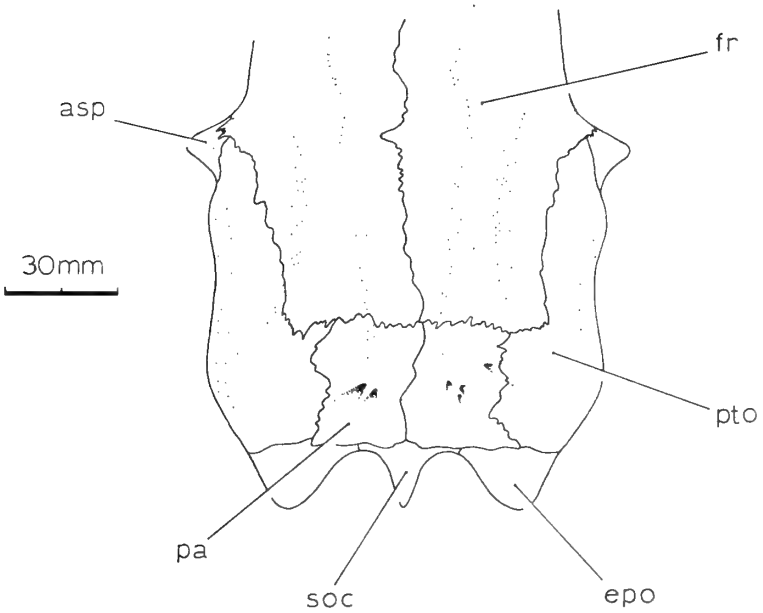

FIG. 35. *Protarpon priscus* (Woodward). Neurocranium, dorsal view of the otic region. Based on B.M.N.H. P.356.

FORMATION AND LOCALITY. London Clay (Ypresian) of Sheppey, Kent, England.

DESCRIPTION. *Neurocranium.* The skull roof is flat, marked only by two prominent ridges, which attain their greatest development at the sphenotic level. The mid-line of the skull roof is slightly depressed, an appearance which is enhanced by the presence of these ridges. A smaller specimen, B.M.N.H. P.356, shows weak ridges. By analogy with *Tarpon* and *Megalops* these ridges contained the supraorbital sensory canals. The supraorbital sensory canal is known to pass posteriorly into the parietal bones in *Megalops* and *Tarpon* and a similar situation existed here as evidenced by the pores upon the parietal bones illustrated. In the otic region the roof is parallel-sided, but posteriorly it is produced into three processes ; a median supraoccipital with large epiotic processes on either side.

Each frontal has a square posterior margin and in consequence imparts an ' L '-shape to the adjacent pterotic. The medially united parietals are slightly longer than broad and have a sinuous suture with both pterotics and frontals. The lateral ethmoid is similar to that of *Tarpon.*

In posterior view the pentagonal supraoccipital bears a prominent supraoccipital crest, on either side of which is a slight depression. The epiotic also exhibits a faint depression immediately beneath the epiotic process. This depression is continued upon the exoccipital. The exoccipital is large and meets its fellow of the opposite side above and below the foramen magnum. Laterally the exoccipital forms the

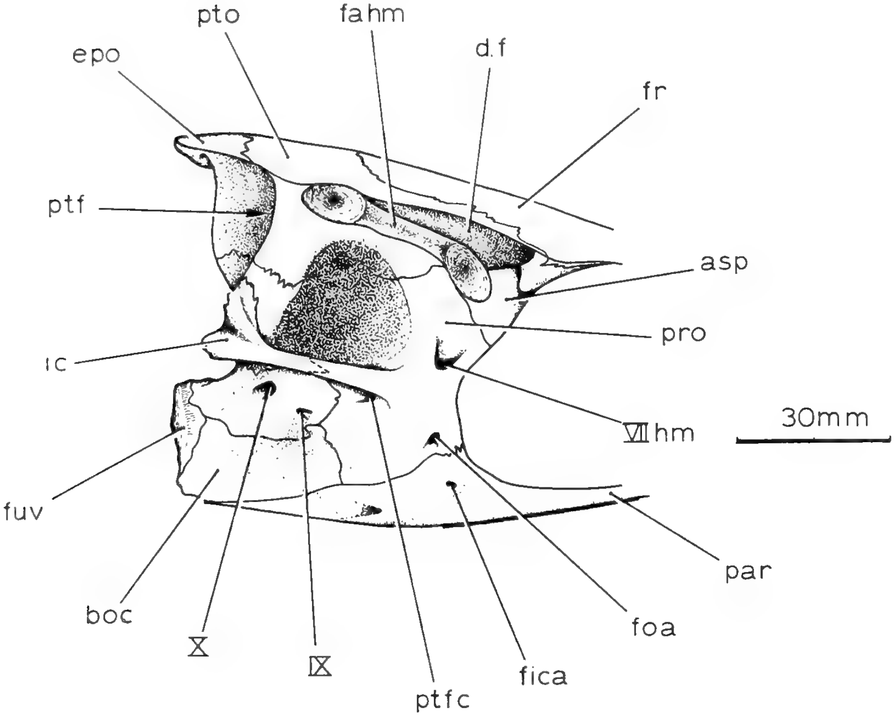

FIG. 36. *Protarpon priscus* (Woodward). Neurocranium, right lateral view of the otic region. Based on B.M.N.H. P.356 and P.26694 (formerly P.1698).

ventral margin to the post-temporal fossa and at this point the bone bears a prominent groove which leads towards, but fails to reach, the occipital condyle. Ventrally the exoccipitals form with the basioccipital a tripartite suture with the first vertebral centrum. This centrum is functionally part of the neurocranium. The centrum exhibits a shallow, asymetrically placed notochord pit. The outer surface of the centrum is generally smooth save for a few longitudinal grooves on its dorsal half. If, as in the Recent megalopids, a neural arch was attached to this element, its union with the centrum must have been weak since there is no evidence of articulatory facets.

A lateral view shows that the neurocranium is deepest at the occiput, a resemblance to *Tarpon*. The dilatator fossa is shallow and roofed by the pterotic which forms much of its inner wall and floor. The hyomandibular facet slopes ventro-anteriorly, there being a slight downward and lateral flexure at the extreme anterior end. The facet consists of two oval depressions linked by a somewhat narrower groove. Like the dilatator fossa the hyomandibular facet is formed largely by the pterotic. The anterior region of both the facet and the fossa is formed by the autosphenotic which is produced laterally as a weakly developed autosphenotic spine.

The subtemporal fossa is large and formed by the pterotic, exoccipital and prootic, which line the dorsal, postero-ventral and antero-ventral regions respectively. It is significant that the anterior border of the subtemporal fossa is ill-defined since this invites comparison with *Tarpon*. The ventral border is clearly demarcated by a prominent prootic-intercalar bridge which stands clear of the underlying exoccipital, leaving a small foramen between the bridge and the lateral cranial wall.

Beneath the subtemporal fossa the exoccipital contacts the basioccipital ventrally and the prootic anteriorly. At the junction of these three bones there is a shallow depression. The depressions of either side are only separated from one another by a double layer of bone and consequently the saccular recesses must have lain above these depressions, as in *Tarpon*. The exoccipital is pierced by two foramina. The larger of these, the vagus foramen, is situated beneath the intercalar and directed postero-ventrally. The smaller glossopharyngeal foramen faces antero-ventrally and is situated in front of and somewhat below the level of the vagus foramen.

The intercalar overlies part of the exoccipital laterally and part of the exoccipital, pterotic and epiotic posteriorly. Much of the intercalar is sutured to the exoccipital. Anteriorly the intercalar is produced as a thin rod to meet a similar projection from the prootic so forming the prootic-intercalar bridge. Posteriorly the intercalar bears a small knob, bordered dorsally and ventrally by grooves, the ventral groove being particularly prominent. The knob of the intercalar probably provided an insertion point for a tendon from the post-temporal. The prootic forms much of the lateral wall of the otic region and is pierced by three large foramina. Ventrally there is a downwardly directed foramen for the orbital artery, dorsally a large upwardly facing hyomandibular foramen, while beneath the prootic region of the prootic-intercalar bridge is the posterior opening of the pars jugularis. This latter

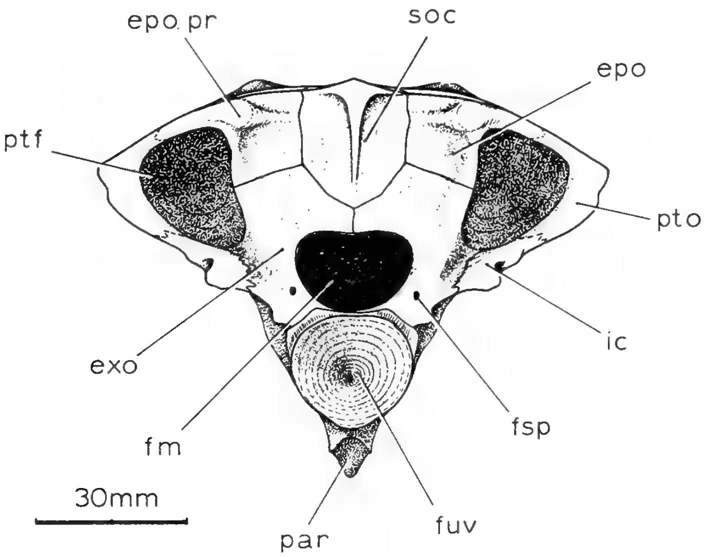

FIG. 37. *Protarpon priscus* (Woodward). Neurocranium in posterior view. Based on B.M.N.H. P.356.

opening is continuous with a short horizontal groove upon the prootic. At the level of the foramen for the jugular vein, the medial surface of the prootic is produced horizontally to meet its partner of the opposite side in the prootic bridge. This bridge is notched anteriorly in the mid-line where it forms the posterior border to the pituitary foramen. The abducens nerve pierced the prootic bridge. The anterior, vertical face of the prootic is pierced by a large trigemino-facialis foramen. The details of the trigemino-facialis chamber are similar to those described for *Tarpon*. Medial to this foramen lies a small oculomotor foramen.

The parasphenoid, which is only seen in one specimen (B.M.N.H. P.26694), extends almost to the posterior end of the neurocranium. Throughout its known extent (i.e. to mid-orbital level) the bone is relatively narrow. Below the orbit the parasphenoid bears a thin row of teeth in the mid-line. The teeth extend posteriorly to beneath the ascending wings. Ventrally the posterior end of the parasphenoid shows a deep median groove which fades anteriorly. A faint lateral groove is seen immediately behind the small ascending wings. The internal carotid foramen lies at the base of the ascending wing.

Hyopalatine bones. Very little is known of this series. The hyomandibular articulates with the neurocranium by a single expanded head which is weakly divided into anterior and posterior regions. The shaft of the hyomandibular is inclined ventrally and slightly posteriorly. Its ventral limit is unknown as it is overlapped by the large metapterygoid. The triangular quadrate is slightly longer than deep and bears a large condylar surface ventrally. Posteriorly the quadrate is deeply grooved and receives the rod-like symplectic. The posterior quadrate border is thick and provided an attachment point for the deeper divisions of the adductor mandibulae musculature. The preoperculum rests against the posterior margin of the quadrate. As in *Tarpon* there is a small notch upon the quadrate immediately behind the articulatory condyle.

Dermal upper jaw. The upper jaw extends from the snout to a level behind the orbit. The oral margin of the jaw is slightly curved, less so than in *Tarpon* or *Megalops*. The premaxilla is relatively small with its oral border equalling one-quarter of the total jaw length. The dorsal border of the premaxilla is produced into a prominence (it hardly deserves the term articular process) which fits into a slight groove upon the head of the maxilla.

The maxilla is a moderately deep, parallel-sided bone, overlain posteriorly by two large supramaxillae which resemble those of *Tarpon*. The head of the maxilla tapers anteriorly before expanding into a dorsal palatine malleolus and an anterior ethmoid prominence.

The oral border of both premaxilla and maxilla bears a thin band of very small villiform teeth. Their posterior extent upon the maxilla is unknown. There appear to be fewer teeth than in either of the Recent megalopids.

Mandible. The mandible projects in front of the premaxilla. The oral border curves slightly upwards from the shallow dentary symphysis. At one-third of the way back the oral border rises more steeply to form a rather elongated coronoid process, as in Recent megalopids. The teeth borne along the oral border are similar to those on the upper jaw.

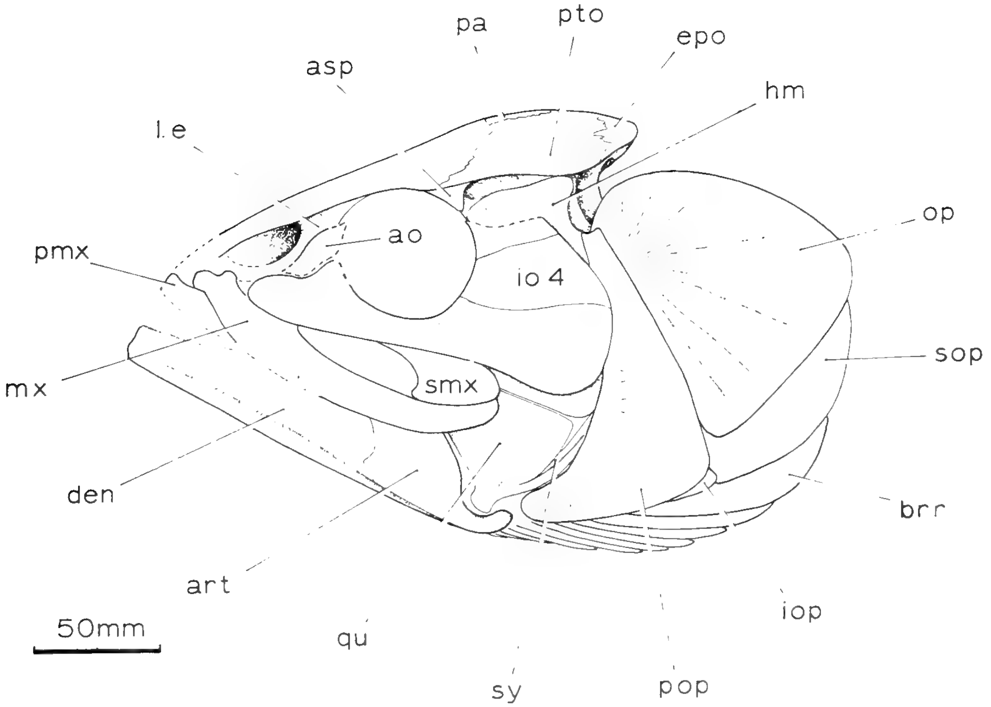

FIG. 38. *Protarpon priscus* (Woodward). Cranium in left lateral view. Based on holotype.

Ventrally the margin of the jaw exhibits a slight inflexion. The surface of the bone in this region is marked by coarse rugae. The dentary forms most of the lower jaw, but posteriorly the articular is produced into a prominent process. The mandibular sensory canal pierced the posterior edge of this process and ran through the mandible opening by small pores which become more numerous nearer the dentary symphysis.

Circumorbital series. The bones of this series are thin and marked only by faint radiating ridges. The first infraorbital is rounded anteriorly and bears a small dorsal prominence which lies posterior to part of the trapezoidal antorbital bone. The antorbital is considerably larger than, and of a different shape from, that element in *Tarpon* and *Megalops.* Beneath the orbit the infraorbital bones are narrow but the extent of the second cannot be seen. The third, fourth and fifth members of the series are broad, extending posteriorly over the preoperculum.

The infraorbital sensory canal runs within the infraorbitals close to the orbital margin, giving off short branches posteriorly. Within infraorbital 1 these branches are numerous and directed posteriorly.

Opercular series. As a consequence of the posterior quadrate/mandibular articulation the preoperculum is composed essentially of a ' vertical ' limb. The bone is narrow dorsally, but ventrally it widens considerably. The concave anterior margin of the preopercular is thickened mid-way along its length to receive part of the superficial adductor mandibulae musculature. The preopercular sensory canal ran close to the anterior margin and opened to the surface of the bone by several large pores.

The operculum is a large bone showing a rounded dorsal margin. The ventral margin is inclined. Like the other opercular bones the surface is marked by ridges radiating from the centre of ossification. The suboperculum continues the contour of the operculum and is partially overlapped by the latter. An interoperculum is present beneath the preoperculum.

There are at least 20 branchiostegal rays. The posterior members of the series are broad and bear the same surface markings as the opercular bones. The anterior branchiostegal rays are fine and needle-like and when the mouth was closed the anteriormost branchiostegal rays were situated beneath the level of the first infraorbital.

Between the lower jaw rami and overlying the anterior branchiostegal rays is a large gular plate, at least half as long as the mandible. The gular plate is widest posteriorly where the width is equal to one-third of its length.

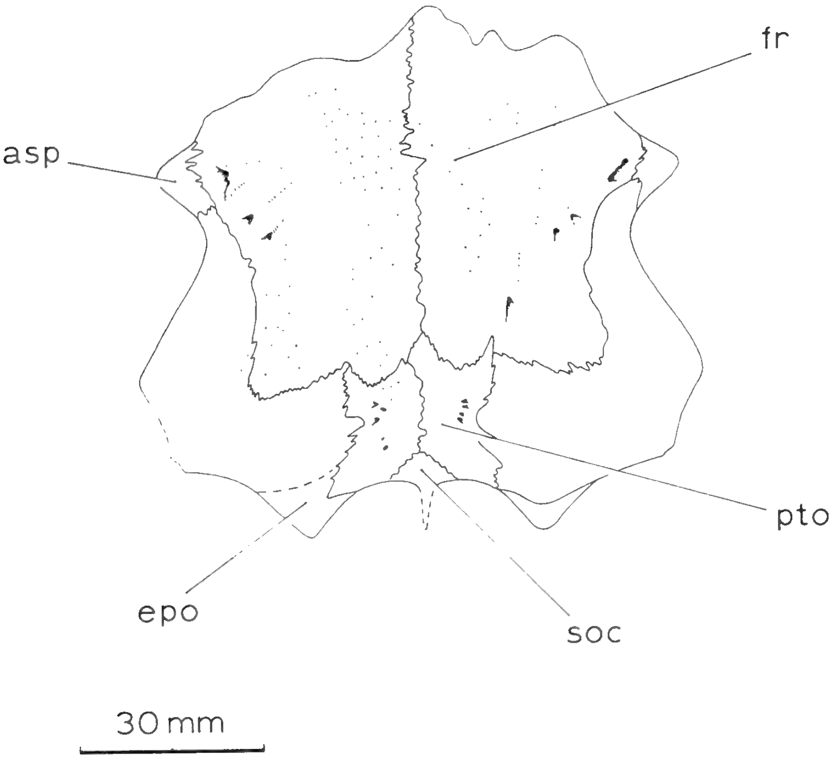

FIG. 39. *Protarpon* cf. *priscus*. Neurocranium, dorsal view of the otic region. From B.M.N.H. P.4153.

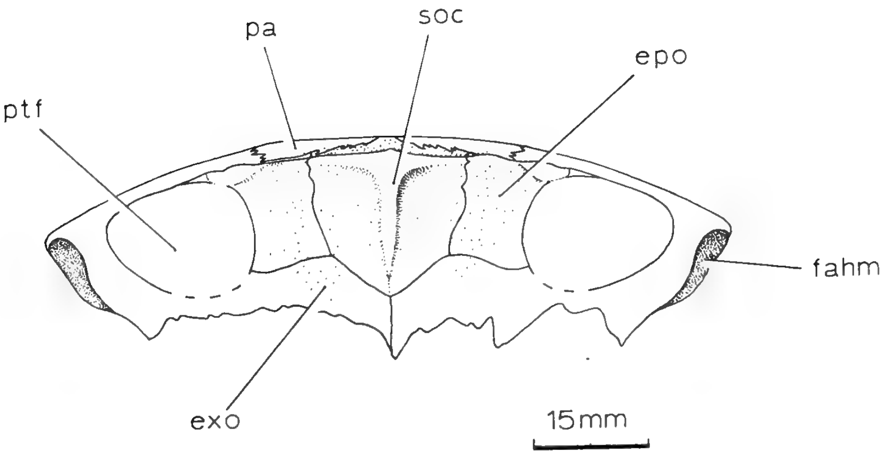

FIG. 40. *Protarpon* cf. *priscus*. Neurocranium, posterior view of dorsal third. From B.M.N.H. P.4153.

Appendix to *Protarpon priscus*

B.M.N.H. P.4153 was considered to be *Megalops priscus* by Woodward (1901 : 26, pl. 3, fig. 6) and Casier (1966 : 118). This specimen consists of the rear part of a neurocranium and although incomplete, it differs somewhat from the typical *P. priscus*. In dorsal view not only is the skull roof relatively wider at the sphenotic level, but the widest point of the neurocranium occurs towards the posterior end of the hyomandibular facet, and not, as in *P. priscus*, at the sphenotic level. The parietals are relatively smaller and exhibit a characteristic ' waisted ' appearance. In posterior view the openings of the post-temporal fossae are circular and not vertically elongated as in *P. priscus*.

Laterally the neurocranium (Woodward 1901 : pl. 3 fig. 6) shows a large, deep dilatator fossa containing a large foramen which probably communicated with the post-temporal fossa. The hyomandibular facet is divided into anterior and posterior oval depressions, linked by an extremely narrow ledge of bone. Finally, the subtemporal fossa appears slightly smaller in area, resembling that of *Megalops*.

The points mentioned are at variance with the neurocranial details seen in the (admittedly few) specimens of *P. priscus* and appear sufficient to remove this specimen (P.4153) from *P. priscus*. However, apart from the neurocranium nothing else is known about this form and in consequence it would not be justifiable to erect a new species for it. Pending a better knowledge of the ontogenetic and individual variation of *P. priscus* (which could only be gained by more specimens) and/or more complete material of forms like P.4153, it seems best to regard this specimen as a form very much like *P. priscus* but possibly representing a different species.

Protarpon oblongus (Woodward)

1844 *Hypsodon oblongus* Agassiz : **5**, pt. 1 : 101 (*nom. nud.*).
1901 *Megalops oblongus* Woodward : 26.
1966 *Megalops oblongus* Woodward ; Casier : 119, pl. 13, fig. 2.

Diagnosis. See Woodward (1901 : 26).

Holotype. B.M.N.H. P.634, an otic region of a neurocranium, rather poorly preserved.

Material. Only the holotype is known.

Formation and locality. London Clay (Ypresian) of Sheppey, Kent, England.

Remarks. This species is retained with reservation. Woodward (1901) distinguished it on the basis that the distance from the occiput to the level of the sphenotic spines is equal to the width at the sphenotics. Although the precise distance between the sphenotic spines cannot be measured in B.M.N.H. P.634 (the lateral roof margins are broken in the specimen) Woodward's distinguishing character remains essentially true.

In the Recent *Tarpon* the proportions of the posterior part of the skull roof change slightly throughout ontogeny, there being a slight increase in length relative to width. However, in *P. priscus* the occiput-sphenotic distance never exceeds 75 per cent of the intersphenotic distance, and is thus very different from that seen in *P. oblongus*.

Casier (1966 : 119) cites the more weakly developed frontal depression and the convergence of the ridges on the skull roof as further differences from *P. priscus*, but in view of the great variability of these features in the genus *Protarpon* it seems best to ignore them.

The parietal bones of *P. oblongus* are only partially preserved, yet enough remains to indicate that their length exceeded twice their width, as in *Tarpon*, whereas the parietals of *P. priscus* are only slightly longer than wide. However during the growth of *Tarpon* the shape of the parietals changes from square to rectangular. The lateral otic wall of the neurocranium is very similar to that of *P. priscus*.

In view of the ontogenetic changes seen in *Tarpon* it could be argued that *P. oblongus* is merely an older individual of *P. priscus*, but the small difference in size between *P. priscus* and *P. oblongus* could not account for the considerable differences in proportions mentioned above. Irrespective of the true specific identity, the important fact remains that the otic region is very similar to *P. priscus* in the roofed dilatator fossa, hyomandibular facet, large subtemporal fossa and the position of the vagus and jugular foramina.

Discussion of the genus *Protarpon*

Protarpon is clearly a member of the Megalopidae. With these fishes it shares such characters as a deep neurocranium with an otic depression comparable to that receiving the swimbladder in Recent forms ; very large post-temporal fossae ; large, prominent epiotic bones ; narrow, virtually edentulous parasphenoid ; and general characters of the ethmoid region (preservation of this region precludes detailed comparison). The jaw structure is similar to that seen in the Recent forms, in particular the deep maxilla with the palatine and ethmoid processes situated close together. The convex oral margin shows a similar dentition. In the opercular series, similarities are seen in the preopercular sensory canal. Further points of similarity include primitive features such as small premaxillae, the large gular plate and high number of branchiostegal rays. These last points cannot, of course, be held to indicate relationship, but merely suggest that *Protarpon* has not become specialized in other directions from Recent megalopids.

On the other hand, there are several features suggesting that *Protarpon* should not be included in a Recent genus. *Protarpon* was included by Woodward (1901) in the genus *Megalops* (which included both Recent species). In recent years, workers (Hollister 1939; Greenwood 1970a) have qualified Jordan and Evermann's (1896) allocation of the two Recent species to separate genera. The basis of this separation has been centred upon the swimbladder/ear linkage (Greenwood 1970a) and certain other details of neurocranial anatomy (see diagnosis of Recent forms and the discussion of *M. cyprinoides* included here). The Eocene species differ from both Recent forms in such details and thus must be accorded generic status. The name *Protarpon* has been chosen in the hope that it conveys the idea of greater anatomical similarity to *Tarpon* than to *Megalops*. These differences are noted and discussed below.

The neurocranial roof of *Protarpon* is relatively flat, in contrast to the convex form in Recent species. In these latter forms the cranial convexity is due to a deepening of the post-temporal fossae, which meet above the endocranium. Such a deepening is not apparent in *Protarpon* and may indicate that the post-temporal fossae of either side remained separate from one another. As in the Recent species, the post-temporal fossae probably extended forward to the orbitosphenoids, since these latter bones exhibit a wide dorsal separation. The autosphenotic spine of *Protarpon* is weakly developed and the dilatator fossa small and roofed by the pterotic. This is unlike the condition in extant species where the dilatator fossa is deep. The weak autosphenotic spine is probably correlated with the flat skull roof.

In the otic region of the neurocranium there is a single shallow depression formed by the exoccipital, basioccipital and prootic. This depression may have contained a simple diverticulum of the swimbladder which must have been only slightly more complex than that seen in large specimens of *Elops lacerta* (Greenwood 1970a). The swimbladder in Recent megalopids is received in complex depressions in the lateral cranial wall. That the swimbladder projection was simple in *Protarpon* is suggested by the primitive position of the jugular canal opening, the position of the vagus and glossopharyngeal foramina and the lack of any supporting crista upon the basioccipital. In Recent megalopids the swimbladder has pushed so far forward as to shift the vagus and glossopharyngeal foramina to a higher and more posterior position. In *Megalops* the jugular canal opening has also shifted.

The premaxilla of *Protarpon* is considerably narrower than that of extant megalopids. The mandible is relatively shallow, without a very large coronoid process, and the symphysis does not protrude to any great extent. The dorsal margin of the operculum is smoothly rounded, without the characteristic indentation seen in *Tarpon* and *Megalops*.

In all of the above respects *Protarpon* is more primitive than the Recent megalopids. It shows no specialization that would exclude it from being an ancestor to either or both of the Recent genera. The apparent greater similarity to *Tarpon* rather than *Megalops* can be attributed to the relative primitive nature of *Protarpon* and *Tarpon*. These two last genera share such characters as a relatively shallow neurocranium, with the maximum depth at the occiput, a straight parasphenoid, the primitive position of the jugular foramen and the lack of a bony covering to the swimbladder/ear connection.

Genus ***PROMEGALOPS*** Casier, 1966

1966 *Promegalops* Casier : 120.

Diagnosis (emended). Megalopid fishes in which the neurocranial roof is markedly convex above the cranial vault. Parietals slightly longer than broad. Dilatator fossa shallow, partially roofed by a very thin ledge formed by the pterotic and autosphenotic. Maximum depth of the neurocranium at the level of the autosphenotic. Parasphenoid bent at the level of the ascending wings. Mandible shallow, coronoid process weakly developed. Operculum with antero-dorsal indentation.

Type-species. *Promegalops signeuxae* Casier, 1966.

Promegalops sheppeyensis Casier, 1966

(Text-figs. 41–43)

Remarks. Casier (1966) erected the genus *Promegalops* for two specimens from the London Clay (Ypresian) of Sheppey, Kent, England. For each specimen a new species was erected, *P. signeuxae* (the type-species) and *P. sheppeyensis* (for a specimen formerly included in *Megalops priscus*, B.M.N.H. P.9192). The former is known by a nearly complete head, the latter from a neurocranium. Both have been adequately described by Casier (1966), but apart from referring the genus to the Elopidae (including the Megalopidae) he came to no definite conclusions about the affinity of this genus.

The megalopid nature of *Promegalops* is shown by the deep skull with a lower jaw which is obliquely inclined towards the snout ; a dentary symphysis which protrudes slightly ; the otic region of the neurocranium which is short and deep ; and by the dermethmoid and mesethmoid which have a similar shape to that seen in Recent megalopids (Casier 1966 doubts the presence of the postero-ventral projection of the ethmoid which occurs in the Recent species).

Promegalops differs from the contemporaneous *Protarpon* in the following important respects : skull roof markedly convex above the cranial vault ; autosphenotic spine moderately well developed ; dilatator fossa shallow and partially roofed by a very thin ledge of the pterotic and autosphenotic ; neurocranium deep, with the maximum depth at the level of the autosphenotic ; parasphenoid bent beneath the level of

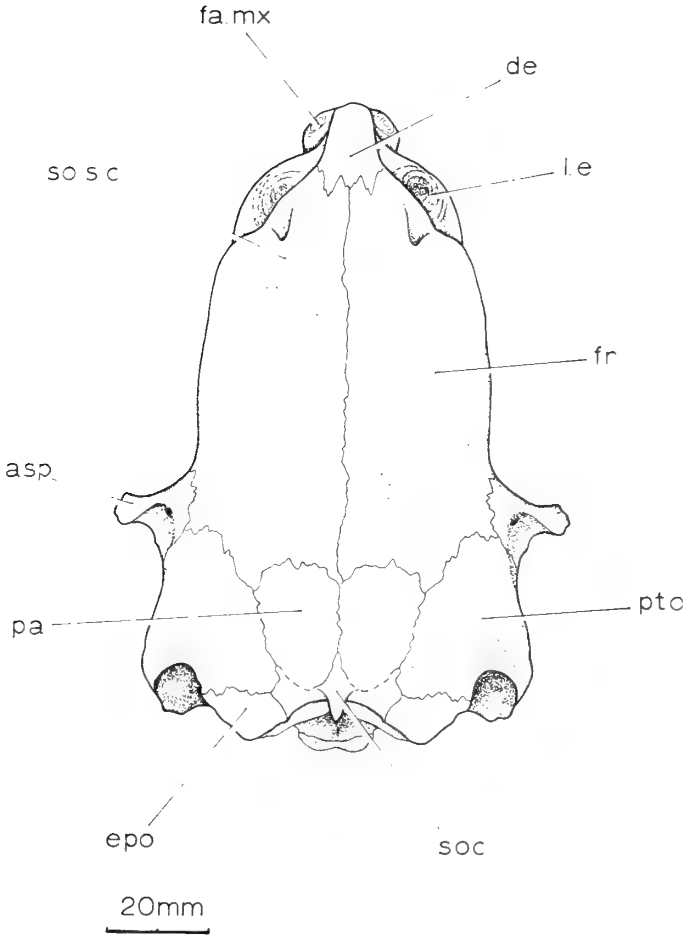

FIG. 41. *Promegalops sheppeyensis* Casier. Neurocranium in dorsal view. From holotype.

the ascending wings ; the quadrate/mandibular articulation lies beneath the middle of the orbit (only known in *P. signeuxae*) ; lower jaw protrudes beyond the premaxilla (only known in *P. signeuxae*) ; operculum exhibits an antero-dorsal indentation (only known in *P. signeuxae*).

In all these respects *Promegalops* is more advanced than *Protarpon*, and is intermediate between *Protarpon* and *Megalops*.

Promegalops differs from *Tarpon* in the deep neurocranium, the angled parasphenoid and the general proportions of the otic region of the neurocranium. Such features are found in *Megalops* and are considered to be advanced. Despite the close similarity between *Promegalops* and Recent Megalopidae (in particular *Megalops*) there are certain features of the Eocene species which may be considered primitive or diagnostic. Primitive features include the shallow lower jaw, with a low,

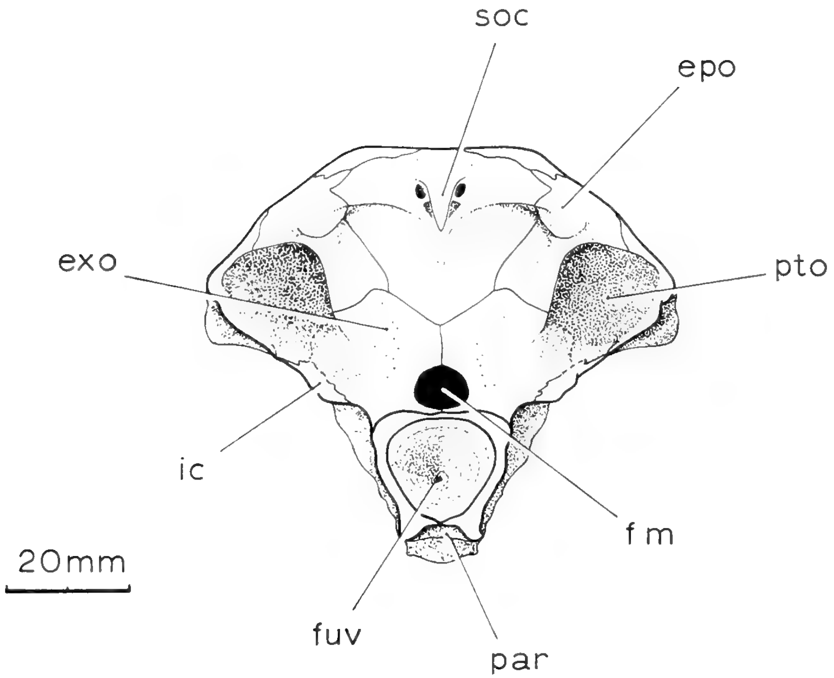

FIG. 42. *Promegalops sheppeyenis* Casier. Neurocranium in posterior view. From holotype.

posteriorly placed coronoid process, and the unexpanded post-temporal. Diagnostic features include the wide frontals, small nasals, and the presence of a large foramen (or foramina in *P. sheppeyensis*) at the base of the dilatator fossa.

In short, *Promegalops* probably evolved from a form resembling *Protarpon* and could be ancestral to *Megalops*, from which it is known to differ only in the wide frontals, partially roofed dilatator fossa, the single depression in the otic region receiving the swimbladder diverticulum, the unexpanded post-temporal and the shallow lower jaw.

Genus ***ELOPOIDES*** Wenz, 1965

DIAGNOSIS (emended). Megalopid fish in which the head is almost as deep as long. Neurocranial roof moderately convex above the otic region. Parietals slightly broader than long. Dermal cranial bones coarsely ornamented with rugae. Orbit large, the diameter exceeding the preorbital distance. Maxilla extending behind the eye. Depth of the operculum exceeding twice its maximum width. Scales large, with seven to eight anterior (basal) radii.

TYPE AND ONLY SPECIES. *Elopoides tomassoni* Wenz.

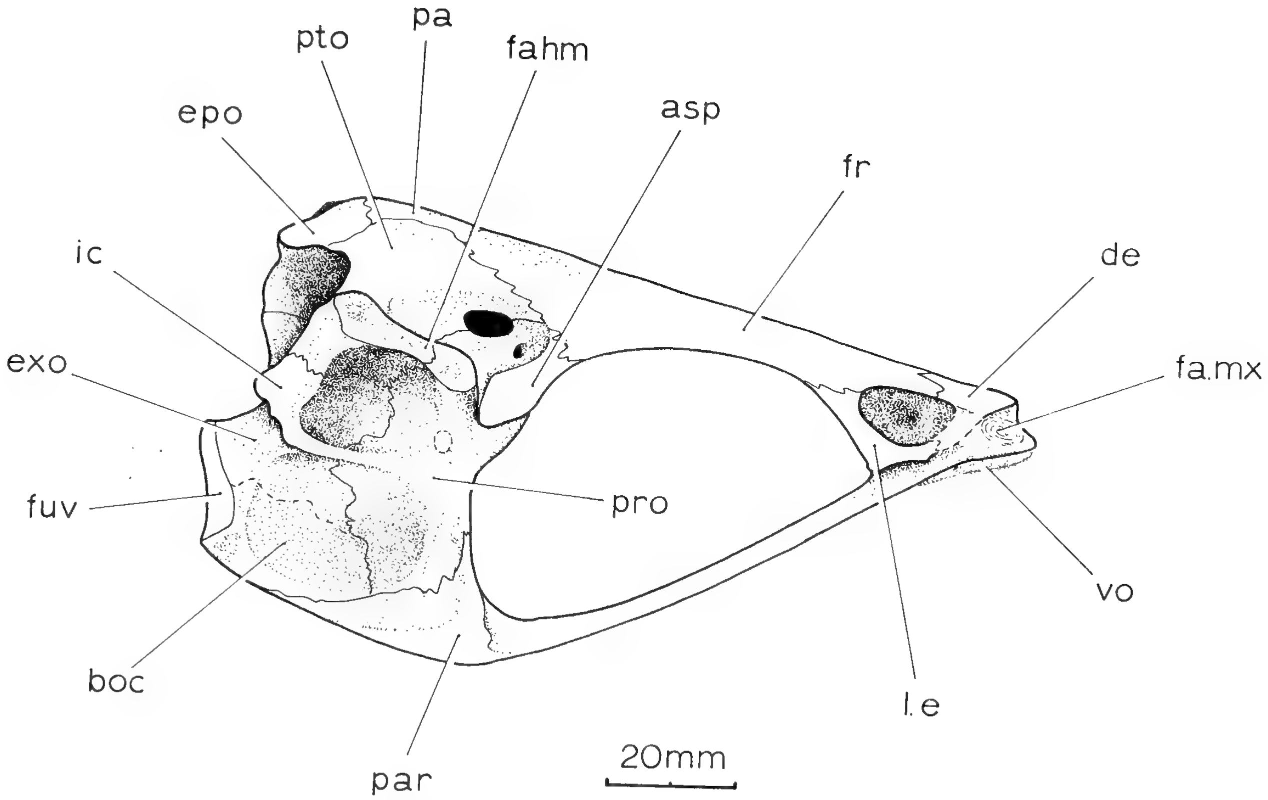

FIG. 43. *Promegalops sheppeyenis* Casier. Neurocranium in right lateral view. From holotype, partially reconstructed. Dotted circle indicates position of VII hm.

Elopoides tomassoni Wenz

1965 *Elopoides tomassoni* Wenz : 4, text-figs. 1, 2, pl. 1, figs. A–E.

DIAGNOSIS. As for genus, only species.

HOLOTYPE. M.H.N.P. 1961–14–1 from the Upper Albian of Vallentigny, France.

REMARKS. No material was examined, but the illustrations given by Wenz (1965 : pl. 1, figs A–E) are adequate for the assessment of the systematic position of this species. Wenz described the anatomy and included *Elopoides* in the family Elopidae (*sensu* Woodward, 1901), indicating that *Elopoides* approached *Holcolepis* (=*Osmeroides*) *lewesiensis*. The similarities between these two genera noticed by Wenz include the relative proportions of the head and body, the position of the fins, number of vertebrae, position of the quadrate/mandibular articulation, the dentition and the absence of enlarged scales at the bases of the paired fins. With the exception of the last these features are also found in other elopoids included by Woodward (1901) in his family Elopidae, and are of doubtful significance in establishing relationship.

Elopoides differs considerably from *Osmeroides lewesiensis*. Wenz (1965 : 12) indicated the following differences : the cranium of *Elopoides* is short and the dorsal profile is steeply inclined, the orbit is large and the preorbital distance is short ; the quadrate/mandibular articulation is situated at the posterior margin of the orbit, and the shape of the dentary is different ; the preoperculum is of different shape ; and the pelvic fins are nearer to the pectorals than in *Osmeroides lewesiensis*. To these differences may be added the shape of the neurocranial roof, the infraorbital series and the opercular apparatus. The numerous differences suggest that *Elopoides* should be removed from association with *O. lewesiensis*.

Several of the features in which *Elopoides* differs from *O. lewesiensis* are points of similarity with megalopids. Thus the cranium is relatively short with respect to the depth. The head of *Elopoides* is in fact relatively deeper than any other megalopid. The otic region of the skull roof is comparatively short and exhibits a moderate convexity, both features seen in Recent megalopids. The greatest width of the cranial roof occurs at the occiput, as in *Tarpon*, whilst the well-developed epiotic process is a typical megalopid feature. The parietals are relatively large and nearly square, resembling the Eocene megalopids and the Recent *Megalops* (*Tarpon* is specialized in possessing elongate parietals). The coarse ornamentation seen upon the dermal bones of *Elopoides* is an unusual feature among megalopids, but is seen in restricted areas in *Protarpon priscus*. The very large pores opening to the supraorbital sensory canal are only found elsewhere among Elopoidei in young specimens of *Elops* and *Megalops*.

The dermal jaws show megalopid features in the deep maxilla with a strongly convex oral border, the large supramaxillae, and the flattened head of the maxilla immediately behind which there is a dome-shaped protuberance, which in Recent megalopids articulates with the palatine medially and the first infraorbital laterally. The mandible, as in megalopids, exhibits a deep coronoid process and a well-developed ‘ retroarticular process ’ fitting into a shallow depression developed on the quadrate behind the articulatory condyle. The symphysis of the lower jaw is shallow as in the Eocene *Protarpon* and *Promegalops* and is unlike the deepened symphysis of Recent megalopids. The lower jaw of *Elopoides* does not protrude beyond the upper jaw. Wenz describes and figures an area of very small teeth on the lateral surface of the dentary. In this respect *Elopoides* is very unusual, not only among megalopids but also among teleosts in general. It may be that this tooth patch represents a detached tooth plate.

In the opercular apparatus, there is both similarity with, and difference from other megalopids. The preoperculum is similar in showing very little curvature and no ventro-posterior expansion. The operculum, however, is unusual in being considerably deeper than wide, imparting a narrow appearance to the opercular series as a whole.

Very little is known of the pectoral girdle and thus comparison is difficult. The post-temporal, however, appears to be a wide, plate-like bone as in most other megalopids. The scales are large, deeply overlapping and marked by fine circuli with ornamentation in the form of fine tubercules confined to the exposed field, adjacent to a centrally placed nucleus. This form of scale is characteristic of the Megalopidae.

The above facts suggest that *Elopoides* be placed in the Megalopidae, differing from these fishes only in the shape of the operculum. In cranial proportions, relative orbital size and scale morphology *Elopoides* is more reminiscent of *Megalops* than *Tarpon*.

Genus ***SEDENHORSTIA*** White & Moy-Thomas, 1940

1863 *Microcoelia* Marck : 48, *non* Guenée 1852 (Lepidoptera).
1940 *Sedenhorstia* White & Moy-Thomas : 396.

Diagnosis (emended). Megalopid fishes in which the neurocranial roof is slightly convex. Dilatator fossa broad, shallow and without a roof. Maximum depth of the neurocranium at the occiput. Upper and lower jaws with a single row of small, pointed teeth. Mandible shallow, with a weakly defined, posteriorly situated coronoid process. Small, hook-shaped ossifications lying in the mid-dorsal line between occiput and origin of the dorsal fin. Scales small, with four to five anterior radii. Exposed field marked by fine granulations arranged in radiating lines.

Type-species. *Microcoelia granulata* Marck from the Campanian of Sendenhorst, Westphalia, Germany.

Material. The following specimens in the B.M.N.H. were examined. *Sedenhorstia dayi* (Hay) as represented by P.13885, P.13893, P.47513, P.47920–21 (part and counterpart), P.13886, all from the Middle Cenomanian of Hajula, Lebanon. The last-mentioned specimen had been prepared in acetic acid. *Sedenhorstia* sp. represented by P.9985 from the Middle Cenomian of Hajula. *Sedenhorstia orientalis* Goody, represented by the holotype P.9983, an acid-prepared specimen from the Middle Cenomanian of Hajula. *Sedenhorstia libanica* (Woodward) represented by P.4865 from the Middle Cenomanian of Hakel, Lebanon.

REMARKS. The genus *Sedenhorstia* contains four species. *S. granulata* (Marck) from the Campanian of Sendenhorst, *S. libanica* (Woodward) from the Middle Cenomanian of Hakel, Lebanon, and *S. dayi* (Hay) and *S. orientalis* Goody, both from the Middle Cenomanian of Hajula, Lebanon.

The Lebanese species are the best known and have been the subject of a study by Goody (1969a) who removed the genus from the Scopelidae (*sensu* Woodward 1901) to the suborder Elopoidei. Goody (1969a) described *S. dayi* in some detail and indicated many similarities with Recent *Elops* and *Megalops*, although no indication was given as to which of these Recent forms it was more nearly related. Goody (1969a) suggested that the genus be placed in a monotypic family, the Sedenhorstiidae, based upon the presence of ossifications within the dorsal median ligament between the occiput and the origin of the dorsal fin. The establishment of a separate family, equal in status to the Megalopidae and Elopidae, seems unjustified on this basis alone, particularly as calcification within the dorsal ligament is not unique to *Sedenhorstia* (Goody 1969a : 20–21). A survey of the characteristics of *Sedenhorstia* indicates affinity with the Megalopidae and it is suggested that the genus be placed in this family. The salient points are discussed below.

The general body form of *Sedenhorstia* resembles that of the Recent megalopids rather than elopids ; the cranium is moderately deep with respect to its length, the orbit is large and the mouth is almost superior. The body was probably slightly compressed, as evidenced by the straight pleural ribs which nearly encircle the abdominal cavity. In megalopids the body is also compressed while in the Elopidae it is rounded. The vertebral column is composed of approximately 50 vertebrae of which 25 are caudal and is similar to *Tarpon* in which there are 53–57 vertebrae of which 20–24 are caudal. *Megalops* exhibits a higher count (*c.* 68) and is thus like *Elops* species in which the count varies from *c.* 63 in *E. machnata* to *c.* 80 in *E. saurus*.

The dorsal fin is situated more posteriorly than in *Elops* or the megalopids and is composed of more rays (23). In this respect *Sedenhorstia* is distinctive. The anal fin, however, is decidedly megalopid in being long and composed of at least 22 rays. The first anal pterygiophore is also similar to *Megalops* and *Tarpon*, exhibiting a close approximation with the vertebral column. The typical megalopid feature of an elongate terminal dorsal and anal lepidotrich is not seen in *Sedenhorstia*. The origin of the pelvic fin in *Sedenhorstia* occurs anterior to the level of the dorsal fin origin (in *S. orientalis* the pelvic and dorsal origin are at the same level), and is thus similar to *Tarpon*.

The caudal skeleton is of the basic elopoid (or leptolepid) type. In possessing a half spine upon the second preural centrum *Sedenhorstia* is primitive (Patterson 1968b) and resembles *Elops* rather than *Megalops* or *Tarpon*, but some specimens of *Megalops* do show a half spine and perhaps little significance can be attached to this feature in this instance. The base of the first uroneural is unforked and no urodermal has been found, conditions which are unlike *Elops* but in accordance with megalopids. A typical megalopid feature of *Sedenhorstia* is the retention of fringing fulcra on the upper margin of the caudal fin. *S. dayi* possesses three such elements while there are five in *S. libanica*. In the number of fringing fulcra *Sedenhorstia* therefore resembles *Megalops* rather than *Tarpon* in which there are rarely more than two.

The neural arches of the first ural and first preural centra are fused in *Sedenhorstia*, producing a single median expansion which Goody (1969a : 19) suggested may be the forerunner of a stegural. Megalopids and *Elops* always show distinct neural arches on these two centra, but in older specimens of the Recent genera there is only a slight indication of their individuality. It would therefore seem that the consolidation in *Sedenhorstia* is of minor significance.

In the cranium there is a general resemblance to megalopids. The skull is relatively deep with the quadrate/mandibular articulation beneath the orbit. *S. orientalis* is unusual among the *Sedenhorstia* species in that the lower jaw articulation occurs immediately behind the orbit. In this respect this species shows an intermediate condition between *Tarpon* and *Elops*. The orbit of *Sedenhorstia* is relatively large and the long basisphenoid pedicel in *S. dayi* suggests a deep myodome, as in *Megalops*. The otic region of the neurocranium is relatively short, as in *Megalops*, and the skull roof in this region exhibits a certain convexity suggesting large post-temporal fossae. Recent megalopids show an open dilatator fossa which is deep in the dorso-ventral plane. Such a fossa, also seen in *Sedenhorstia*, differs from the shallow, roofed fossa in *Elops*. The Eocene megalopids more nearly resemble *Elops* in this respect.

The parasphenoid of *Sedenhorstia* appears to be edentulous. If teeth were present they must have been very small and restricted to the mid-line beneath the basisphenoid pedicel. A nearly edentulous parasphenoid is found in megalopids, but not in *Elops*.

The upper jaw shows a marked convexity along the oral border and is relatively deep, with two very large supramaxillae. Anteriorly the maxillary head shows a simple ethmoid projection immediately behind which there is a rounded process articulating with the palatine. In all these features there is a close agreement with the megalopids. A further megalopid feature of the upper jaw is the extension of the premaxilla beyond the dermethmoid. The maxilla of *S. orientalis* resembles that of *Elops* in its length, extending well behind the orbit. The lower jaw is similar to *Elops*, *Protarpon* and *Promegalops* in remaining moderately shallow throughout its length, with an ill-defined coronoid process. The Recent megalopids have a prominent coronoid process, which is elongated antero-posteriorly. The teeth on the dermal jaws are unusual among elopoids in being pointed and set in a single row.

The circumorbital bones are relatively narrow and the fifth tapers dorsally, as in megalopids. The fifth infraorbital is rectangular in *Elops*. The first infraorbital shows a gently rounded dorsal margin, as in megalopids. In *Elops* the first infraorbital turns upwards to lie alongside the supraorbital. The number of infraorbitals is constant throughout the elopids and megalopids. Goody (1969a : fig. 1) shows six infraorbitals (one more than is usual) in *S. dayi* but this appears to be an error.

In the opercular series the preoperculum is narrow with the dorsal limb inclined antero-ventrally (or vertically in *S. orientalis*), as in megalopids. The preopercular sensory canal opens to the surface by a series of large pores. In *Elops* the upper preopercular limb is inclined postero-ventrally and the sensory canal opens by a series of short secondary branches, each with a terminal pore.

The scales are relatively small, unlike those of megalopids, and are thin and cycloid. The presence of bone cells has not yet been demonstrated. The anterior field is marked by 4–5 radii resulting in 3–4 scallops along the anterior margin. *Tarpon* usually exhibits 4 radii, while *Megalops* shows about 6. *Elops* and *Davichthys* scales show at least 11 radii. The ornamentation of the exposed field is like the Eocene megalopids in showing a fine granulation composed of minute tubercles. A point of distinction is that the granulations in *Sedenhorstia* appear to be arranged in radiating lines. The exposed surface of elopid scales is unornamented except for the area immediately adjacent to the nucleus.

It is regrettable that the ethmoid and intercalar of *Sedenhorstia* are not well known, for it is in these areas that the megalopids are most clearly characterized. Nevertheless, the features referred to above serve to establish that *Sedenhorstia* exhibited a morphology comparable with that of the Megalopidae. Features of the dentition and perhaps the peculiar ossifications in the dorsal ligament divorce *Sedenhorstia* from the main megalopid line, but its close alliance with this lineage seems certain. The phylogenetic position of *Sedenhorstia* is further analysed in the general discussion of the Megalopidae (p. 201).

Genus ***PACHYTHRISSOPS*** Woodward, 1919

? 1914 *Parathrissops* Eastman : 423 (name preoccupied : *Parathrissops* Sauvage, 1891 : 37).
1919 *Pachythrissops* Woodward : 128.

DIAGNOSIS. See Woodward (1919).

REMARKS. The genus is briefly discussed following a proposal by Nybelin (1964) that at least one of the contained species shows a resemblance to *Megalops*.

The genus *Pachythrissops* is known from three species. The type-species, *P. laevis* Woodward, is from the Upper Portlandian of Dorset, England ; *P. vectensis* Woodward is from the Weald Clay (?L. Aptian) of the Isle of Wight, England, and *P. propterus* (Wagner) is from the Kimmeridgian of Solenhofen, Germany. Questionably, the so-called *Parathrissops furcatus* Eastman is also placed in this genus.

Several complete specimens of the type-species were examined together with two specimens of *P. vectensis* and one specimen (B.M. N.H. 37056) which is probably a young individual of *P. propterus*.

DISCUSSION. During a revision of the genus *Thrissops* Agassiz, Nybelin (1964) briefly described *P. propterus* and suggested that it was only remotely related to *Thrissops* and *Allothrissops*. The latter genera are considered to be related to the Ichthyodectidae. Furthermore, Nybelin tentatively proposed that *P. propterus* may be an ancestor of *Megalops*, quoting similarities in premaxillary dentition, caudal fin fulcra and other unspecified characters.

Bardack (1965) included *Pachythrissops* (recognizing the type-species as *P. propterus*) in the family Chirocentridae (*sensu* Saint-Seine 1949) and endorsed Nybelin's views, quoting the presence of a gular plate in *P. propterus* as further evidence for separating this species from *Allothrissops* and *Thrissops*. Bardack

(1965 : 34) also stated that *P. propterus* is generically distinct from the English species. In support of this statement Bardack refers to five points of dissimilarity between the English and Solenhofen species : the proportions of the body ; structure of the neurocranium ; form of the dentition ; number of vertebrae and the relative positions of dorsal and anal fins. I have been unable to examine ' typical ' specimens of *P. propterus* but the description and figures given by Nybelin (1964) are sufficient to invalidate the above points. Firstly, the body proportions are very similar in both the English and Solenhofen species and differ somewhat from *Thrissops* and *Allothrissops*. The head length of all *Pachythrissops* species is contained approximately four times in the standard length and thus differs from the contemporaneous ' chirocentrids ' in which the head length never exceeds one-fifth of the standard length. In the body depth there is virtually no difference between *P. laevis* and *P. propterus* whereas *P. vectensis* appears slightly more slender. The relative depth of the cranium is also similar in all the species of *Pachythrissops*.

The unspecified differences in neurocranial structure mentioned by Bardack (1965 : 34) are equally difficult to understand. The degree of ' similarity or difference ' in neurocranial structure may be taken at various levels depending on how well the neurocrania are known. None of the *Pachythrissops* species is well known and in consequence comparison must be at a superficial level. In as much as the English and Solenhofen species show shallow neurocrania with a flat roof and a straight, edentulous parasphenoid, with a weak development of the lateral ethmoid region, there is a degree of resemblance. Such resemblances are of a primitive nature with the exception of the weakly developed lateral ethmoid, and are found in other contemporaneous teleosts.

The number of vertebrae is similar in *P. laevis* and *P. propterus* ; the count for *P. vectensis* is unknown. *P. laevis* shows 53–56 vertebrae of which approximately 22 are caudal. According to Nybelin (1964 : 34) *P. propterus* has 50–54 vertebrae (24–25 caudal).

The differences in the relative positions of dorsal and anal fins (Bardack 1965) appear to be erroneous. In both *P. laevis* and *P. propterus* the fins are posteriorly placed and the dorsal fin originates slightly anterior to the anal fin. The slight difference in the position of the dorsal fin in these two species is of minor importance since it is often subject to specific and even ontogenetic variation.

Further points of similarity between the English and Solenhofen species are seen in the jaws. The premaxilla forms nearly one-third of the oral margin of the jaw. The dentary exhibits an inflected ventral margin and the oral margin rises steeply to produce an elongate coronoid process (this feature is seen in several other contemporaneous teleosts, e.g. *Allothrissops* and *Leptolepis*). The dentition is represented by a band of small teeth upon the premaxilla, maxilla and dentary. Those of the dentary become slightly larger at the symphysis. Saint-Seine (1949) attributed large toothed forms to *Pachythrissops* and concluded that this genus was carnivorous. It is probable that the specimens he attributed to *Pachythrissops* were in fact *Thrissops formosus*.

The above brief notes suggest that there is, at present, no basis for separating *Pachythrissops propterus* from the English species.

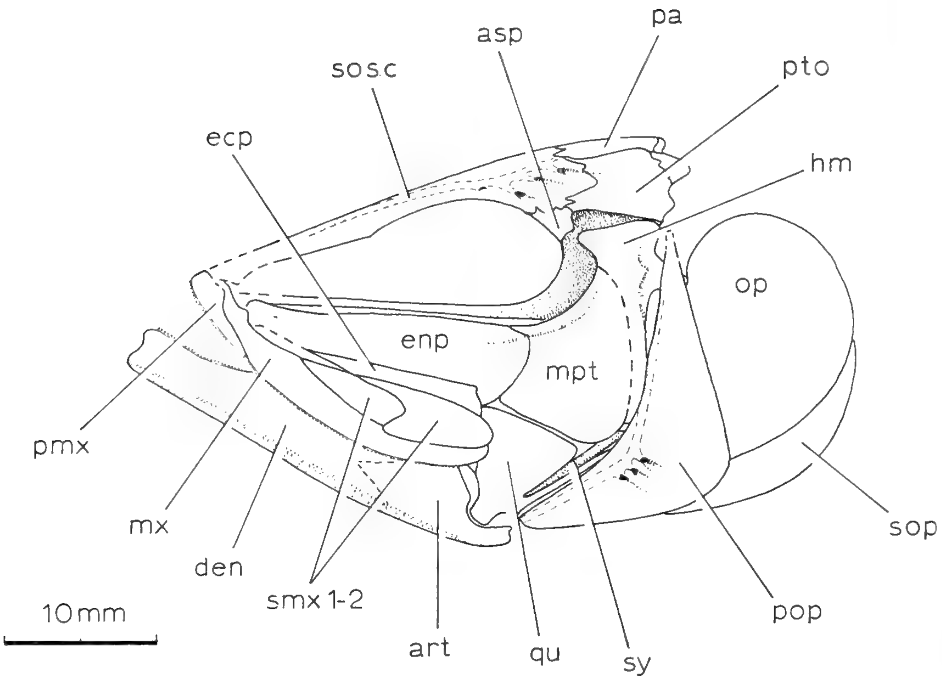

FIG. 44. *Pachythrissops laevis* Woodward. Cranium in left lateral view. Composite of several B.M.N.H. specimens.

The systematic position of *Pachythrissops* presents many problems, which stem from the extreme primitiveness of this form (a phenomenon not unknown in this work). An association of *Pachythrissops* with *Allothrissops* and *Thrissops* seems unlikely and the suggestion that *Pachythrissops* is a stem ichthyodectid (Saint-Seine 1949) is untenable.

Some of the characters which unite *Allothrissops* and *Thrissops* with one another and with the ichthyodectids include the following :

i. Body form elongate with a small, deep head and an elongate anal fin originating anterior to a short-based dorsal fin.
ii. Pectoral fin with the outer rays somewhat enlarged and flattened.
iii. Vertebrae marked with a prominent longitudinal strut.
iv. Apparent lack of epipleural intermuscular bones.
v. Dentition in the form of a single row of small (*Allothrissops*) or prominent conical teeth (*Thrissops*).
vi. The preopercular sensory canal with many long branches extending postero-ventrally in the ventral half of the bone. Although the individual branches may not be seen in the Cretaceous ichthyodectids there is a series of many pores near the ventral margin of the preoperculum indicating that there are long branches from the main preopercular sensory canal.
vii. A stout basipterygoid process ; this is a retained character.

viii. The caudal skeleton contains a series of strap-shaped uroneurals (see below), and in the Cretaceous ichthyodectids further specializations occur in the shape of the hypurals and the posterior neural and haemal spines (Cavender 1966).

In features i–v *Pachythrissops* is more primitive than *Allothrissops* and *Thrissops* and therefore may not be separated from them on these features. However, the last three features indicate that *Pachythrissops* is more advanced than *Thrissops* and *Allothrissops*. The absence of a basipterygoid process in *Pachythrissops* is not definitely established, due to imperfections in preservation, but the several neurocrania of *P. laevis* examined show no evidence of such a process. The preoperculum of *Pachythrissops* differs from *Allothrissops* and *Thrissops* in lacking the distinctive projection at the postero-ventral angle and the preopercular sensory canal opens to the surface by two or three very short branches situated at the angle of the bone. Both of these features are common to many lower teleosts and would not invalidate the derivation of *Pachythrissops* from a form like *Allothrissops* as implied by Bardack (1965 : fig. 3).

The caudal skeleton, however, makes it almost impossible to ally *Pachythrissops* with *Allothrissops* and *Thrissops*. *Pachythrissops laevis* shows four elongate uroneurals and a series of about three smaller elements situated posteriorly. Nybelin (1971) described the caudal skeleton of *P. propterus* and it agrees with *P. laevis*. In both, there is a full-length neural spine on the second pre-ural centrum and four elongate uroneurals. The first uroneural is short and there is a large gap between the second and third hypurals. Such an arrangement cannot have given rise to that of *Allothrissops*, etc., and it is highly unlikely that it was derived from the latter. To justify this statement a broader view of the teleost uroneural series is necessary.

Patterson (1968a) formulated the evolution of the teleost caudal skeleton from the pholidophorid type and described the anatomy of the tail of *Leptolepis coryphaenoides* from the Upper Lias, which may be taken as representing the most primitive teleost stage. The definition of a teleost proposed by Patterson (1968a) is accepted and would thus include *Leptolepis* but exclude *Pholidophorus*. The uroneurals of *L. coryphaenoides* consist of a graded series of six (sometimes seven, Patterson 1968a : fig. 9c) elements, the anterior member of this series extending lateral to the second or third preural centrum.

In the upper Jurassic *Leptolepis dubia* the uroneurals may be divided into two distinct series. The anterior series consists of four strap-shaped elements and these are succeeded by three short uroneurals, the anterior one of which lies lateral to the fourth member of the anterior series. This uroneural arrangement is very characteristic and may be traced through to *Elops*. To attain the *Elops* grade, a fusion of the first with the second, and the third with the fourth uroneurals has to be postulated. There is both circumstantial and direct evidence for this having happened (Patterson 1968a : 226). The third uroneural of *Elops* corresponds to the fifth of *Leptolepis dubia*. The *L. dubia* type of uroneural disposition is probably basic not only for elopoids, but probably for Clupeomorpha and Protacanthopterygii as well, since the two uroneural series are present in the basal members of these groups.

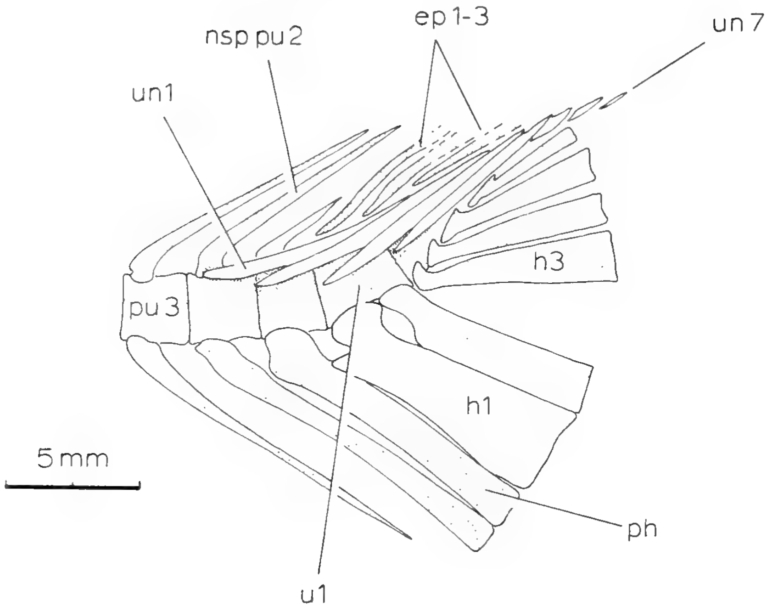

FIG. 45. *Pachythrissops laevis* Woodward. Caudal skeleton in left lateral view. Based on B.M.N.H. 40333 (holotype) and P.29392.

Allothrissops and *Thrissops*, however, have retained the *Leptolepis coryphaenoides* type. Instead of the fifth uroneural remaining short, this and succeeding uroneurals extend basally to lie lateral to the preural and ural centra. Concomitant with this development the anterior uroneurals tend to extend forward and in the Cretaceous ichthyodectids, which also show at least five elongate uroneurals, the anterior members of the series extend as far forwards as the fourth preural centrum. The development of this unique uroneural arrangement is probably correlated with greater rigidity in the tail. The body form of the ichthyodectids suggests fast swimming fishes. The caudal fin is very deeply forked with the caudal fin-rays crossing the hypurals at a steep angle and those of the upper lobe lying in line with the uroneurals. In the Cretaceous ichthyodectids, and to a lesser degree in *Allothrissops* and *Thrissops*, various degrees of hypurostegy are shown. Hypurostegy is by no means confined to the ichthyodectids but is found in several groups of higher teleosts, e.g. Scombridae, yet the combination of this feature with the uroneural development is unique.

The caudal skeleton of *Pachythrissops* is virtually identical with that of *Leptolepis dubia* in showing two distinct series of uroneurals, the anterior group consisting of four uroneurals and the posterior of three. To derive an *Allothrissops*- and *Thrissops*-like caudal skeleton from the *Pachythrissops* type a simplification of the uroneural series would have first to take place, a view with little to recommend it. Alternatively, the evolution of the *Pachythrissops*-type from *Allothrissops* would imply that the evolution of two sets of uroneurals occurred twice, independently and at the same time. This latter view also seems untenable. Thus *Pachythrissops*, on caudal fin anatomy alone, would appear distinct from the *Allothrissops*–*Thrissops*–ichthyodectid lineage.

Removal of *Pachythrissops* from association with *Allothrissops* and *Thrissops* creates the vexatious problem of the true affinity of the genus. The resemblances between *P. propterus* and *Megalops* mentioned by Nybelin (1964) may also be extended to include the English species. Thus the premaxilla bears a band of fine teeth and there are fulcra present on the upper caudal lobe. Other similarities may be found in the lower jaw, where the oral border is concave and is produced to form an elongate coronoid process. Certain resemblances may be seen in the hyopalatine series. The hyomandibular and metapterygoid are similar in shape to those of the Megalopidae and a prominent metapterygoid-endopterygoid ridge is present in the Recent megalopids and *Pachythrissops*. The condyle of the quadrate is succeeded by a shallow but well-marked cup which acts as a stop in the downward movement of the lower jaw.

The posterior face of the neurocranium, known only in *P. vectensis*, exhibits an overall similarity with *Tarpon*. Thus the cranium is deep relative to its width, the openings to the post-temporal fossae are large and the epiotic processes well developed. In the Eocene and Recent megalopids the first vertebra is incorporated with the neurocranium, the exoccipitals and basioccipital forming a tripartite surface for it. In *Pachythrissops* the first vertebra is distinct and the condyle is formed solely by the vertebra-like expansion of the basioccipital, as in *Albula*, *Pterothrissus* and many other 'isospondyls'. In the skull roof certain features agree with *Tarpon* ; the sphenotic spines are prominent and knob-like at their extremities, the parietals are longer than broad, and the dilatator fossa appears virtually open with only a narrow shelf of bone forming a roof. Conversely, there are several differences in the proportions. The skull roof of *Pachythrissops* is narrow, the parietals are ornamented posteriorly and several prominent ridges run longitudinally. The parasphenoid shows the same form as in *Tarpon*, and, as far as can be seen, is edentulous in contrast to the toothed vomer anteriorly.

A single specimen of *Pachythrissops laevis* shows gill-rakers and scattered tooth plates which have become detached from the branchial arch elements. In both features a resemblance is noted with the megalopids.

All these similarities are in primitive features and of little use as evidence of natural relationship. An undisputed megalopid feature is the modification of the intercalar. The intercalar is unmodified in *Pachythrissops*, yet this does not preclude close phylogenetic relationship since it is postulated here that intercalar modification was a relatively late (Eocene) development. As is so often the case one is forced to rely on general appearance, and there is some agreement in superficial features. Thus, *Pachythrissops* is tentatively placed in the Megalopidae but excluded from discussion pending more complete knowledge, not only of the genus itself, but also of contemporary teleosts.

Suborder ALBULOIDEI Greenwood *et al.*, 1966

Diagnosis. Elopiform fishes in which the cranium is shallow and broad at the occiput. Sensory canals developed as a cavernous system, incompletely covered by bone. Ethmoid commissure complete or, more usually, incomplete. Post-temporal fossa small, directed antero-medially. Sub-epiotic fossa well developed. Dilatator fossa narrow, always with a roof. Autosphenotic spine and epiotic process weakly developed. Intercalar small, prootic-intercalar bridge absent. Bulla containing the sacculith large. Otophysic connection absent. Lateral ethmoid in contact with the parasphenoid. Ectopterygoid process well developed. Quadrate/mandibular articulation beneath orbit or lateral ethmoid. Premaxilla forming at least one-third of the upper jaw margin. Mandible with prominent coronoid process, shallow symphysis and a strongly inflected ventral margin. Supratemporal small, not meeting its partner in the mid-line. Caudal skeleton with six hypurals. Scales with dense covering of tubercles in the anterior field.

Family **OSMEROIDIDAE** nov.

Diagnosis. Albuloid fishes in which the snout is not elongated; the mouth is terminal and the ethmoid commissure is complete. Supraorbital sensory canal with a branch running into the parietal. Sub-epiotic fossae demarcated medially by a pronounced ridge. First vertebral centrum incorporated in the neurocranium. Parasphenoid, vomer, dermopalatine, endopterygoid and ectopterygoid with a dense covering of small villiform teeth. Basibranchial and basihyal plates with similar teeth. Supraorbital large. Posterior infraorbitals broad, completely covering the cheek region. Premaxilla without contained sensory canal (in those forms in which the premaxilla is known). Premaxilla and maxilla moving together, both elements bearing a band of villiform teeth. Two supramaxillae. Mandible with coronoid process situated posteriorly; articular and endosteal articular ossified separately. Branchiostegals more than 14 in number. Gular plate large. Dorsal and anal fins short-based. Caudal skeleton in which the second preural neural arch bears a half length neural spine. Three uroneurals. Inner caudal rays of each lobe with expanded bases which overlap the hypurals. Caudal scute present both above and below peduncle.

Genus ***OSMEROIDES*** Agassiz, 1837

1837 *Osmeroides* Agassiz : **5**, pls. 60b, c.
1863 *Rhabdolepis* Marck : 26.
1868 *Holcolepis* Marck : 278 (in part).

Diagnosis. Dermal bones of the cranium stout and heavy, the flat cranial roof with a large dermethmoid. Neurocranium with deep dilatator fossa roofed by pterotic; intercalar reduced to a knob-like protuberance. Parasphenoid stout, connecting (sometimes by suture) with the lateral ethmoid, and, like the pterygoid bones, bearing a large patch of small, villiform teeth set in shallow sockets. Jaw articulation beneath the middle of the orbit. Upper jaw with premaxilla forming about half of the functional oral margin. Supratemporal small and triangular, lying behind the pterotic. Caudal fin with no gap between the second and third hypurals. Body covered by moderately large scales. Scales at the bases of the fins unmodified.

TYPE-SPECIES. *Salmo lewesiensis* Mantell.

REMARKS. Arambourg (1954) maintained that the correct generic name for this form should be *Holcolepis*. In this he has been followed by Wenz (1965). Arambourg stated that *Osmeroides* should be used for the myctophiform fish *Sardinioides* Marck. Goody (1969b) rightly states that the first usage of *Osmeroides* in a binomen was for *Osmeroides lewesiensis* (Agassiz 1837 : **5**, pls. 60b, c) and this precedes the first usage of both *Holcolepis* (Marck 1868 : 278) and *Sardinioides* (Marck 1858).

Osmeroides lewesiensis (Mantell)

(Text-figs. 46–53)

1822 *Salmo lewesiensis* Mantell : 235, pl. 33, fig. 12, pl. 34, fig. 3, pl. 40, fig. 1.
1837 *Osmeroides lewesiensis* (Mantell) Agassiz : **5** ; pt 1, p. 14, pt 2, p. 105, pl. 60b figs. 1, 2, 5, 6, 7 (not figs. 3, 4), pl. 60c.
1838 *Osmeroides mantelli* Mantell : 307, fig. 1.
? 1878 *Osmeroides lewesiensis* (Mantell) ; Fritsch : 32, pl. 7, figs. 5, 6, pl. 8, fig. 1.
? 1885 *Osmeroides lewesiensis* (Mantell) ; Laube : 292, pl. 2, figs. 2, 3 and woodcut.
1888 *Osmeroides lewesiensis* (Mantell) ; Woodward : 322.
1895 *Osmeroides lewesiensis* (Mantell) ; Woodward : 656, pl. 42.
1901 *Osmeroides lewesiensis* (Mantell) ; Woodward : 11, fig. 2.
1964 *Osmeroides lewesiensis* (Mantell) ; Danil'chenko : 398, fig. 104.

DIAGNOSIS (emended). *Osmeroides* attaining 500 mm S.L. Length of cranium equal to twice the maximum width. Parietals longer than broad. Dermal skull bones showing prominent ornamentation in the form of coarse radiating rugae. Large supraorbital firmly united with the frontal. Parasphenoid extending to the rear of the neurocranium. Complete, ossified interorbital septum. Mandibular articulation at mid-orbital level. Branchiostegal rays 18–21 in number, the upper members of the series showing coarse ornamentation. Dorsal fin with 18–20 rays, arising midway between snout and caudal peduncle. Vertebrae as long as deep, marked by irregular longitudinal ridges. Caudal skeleton with four uroneurals and three epurals. Scales large, the posterior field with faint tubercles arranged in radiating rows, anterior field showing about five prominent radii. 15–17 scales in the transverse series immediately anterior to the dorsal fin.

HOLOTYPE. B.M.N.H. 4294, a specimen showing the head and abdominal region from the Upper Cenomanian (*Holaster subglobosus* zone) of Lewes, Sussex, England.

MATERIAL. Twenty-five specimens in the B.M.N.H. were examined. B.M.N.H. P.6456 was prepared in acetic acid and B.M.N.H. 49894 was prepared mechanically. Specimens come from Upper Albian-Coniacian of S.E. England. The Upper Albian record is based on a very imperfect specimen (B.M.N.H. P.8949) from the Gault Clay at Folkestone, Kent. The opercular bones of this specimen are less ornamented than the Chalk specimens but otherwise there is close agreement.

Description. The description of the neurocranium is based mainly upon the acid prepared specimen. Several points were checked against a similarly prepared specimen of *O. levis* Woodward, B.M.N.H. P.36240. The differences between these two species are noted in the remarks on *O. levis*.

The head plus opercular apparatus is equal to 25 per cent of the standard length. The maximum depth of the head occurs at the level of the quadrate/mandibular articulation and is equal to 60 per cent of the head length. The diameter of the orbit is slightly less than the preorbital distance and represents 20 per cent of the head length. The bones of the cranium are thick and the dermal elements are coarsely ornamented.

Neurocranium. The neurocranium is long and shallow, with the cranial vault occupying the posterior third of its length. The greatest width occurs at the occiput and is equal to 50 per cent of the total neurocranial length. In lateral profile the roof is comparatively straight.

Anteriorly the roof of the cranium is formed by a large dermethmoid which, unlike the other roofing bones, is unornamented and smooth. The anterior portion of the dermethmoid is diamond-shaped, with the two antero-lateral margins in close juxtaposition with the premaxillae. In some specimens there are two to four pores aligned transversely across the anterior region of the dermethmoid. This line of pores is interpreted as evidence of a bone-enclosed ethmoid commissure. Posteriorly the dermethmoid extends backwards to the level of the lateral ethmoid and is in syndesmotic union with the frontals, the suture line being ' W '-shaped.

Each frontal is narrow anteriorly but expands above the posterior third of the orbit. Much of the cranial vault is roofed by the frontal which is in contact with the parietal posteriorly and the pterotic posteriorly and laterally. The frontal of either side is united with its partner by a sinuous suture, the meanderings of which increase posteriorly. The path taken by the supraorbital sensory canal within the bone is marked externally by a strong ridge running the length of the orbital section, but posteriorly the ornamentation obscures it. Ornamentation on the frontal (as with the other roofing bones) takes the form of irregular tubercles arranged in sinuous, sometimes anastomosing lines, radiating from the centre of ossification. The ornamentation becomes less conspicuous anteriorly.

The parietal, which joins its partner in the mid-line throughout its length, is rectangular, with the shorter axis transverse. The posterior limit of the parietals is such that the supraoccipital is excluded from the skull roof. Ornamentation is similar to that on the posterior region of the frontal.

The pterotic has three external faces ; dorsal (horizontal), lateral and posterior (both vertical). The dorsal face, which represents the dermal component, shows heavy ornamentation. The roof of both the dilatator fossa and post-temporal fossa is formed by this face. A line of pores running along the lateral edge of the dorsal face marks the path of the otic division of the cephalic sensory canal system. Posteriorly the sensory canal leaves the bone by a single large pore.

The lateral face of the pterotic forms the posterior two-thirds of the hyomandibular facet, part of the inner wall of the dilatator fossa and the dorsal region of the subtemporal fossa. Medially this part of the pterotic forms the lateral wall and floor

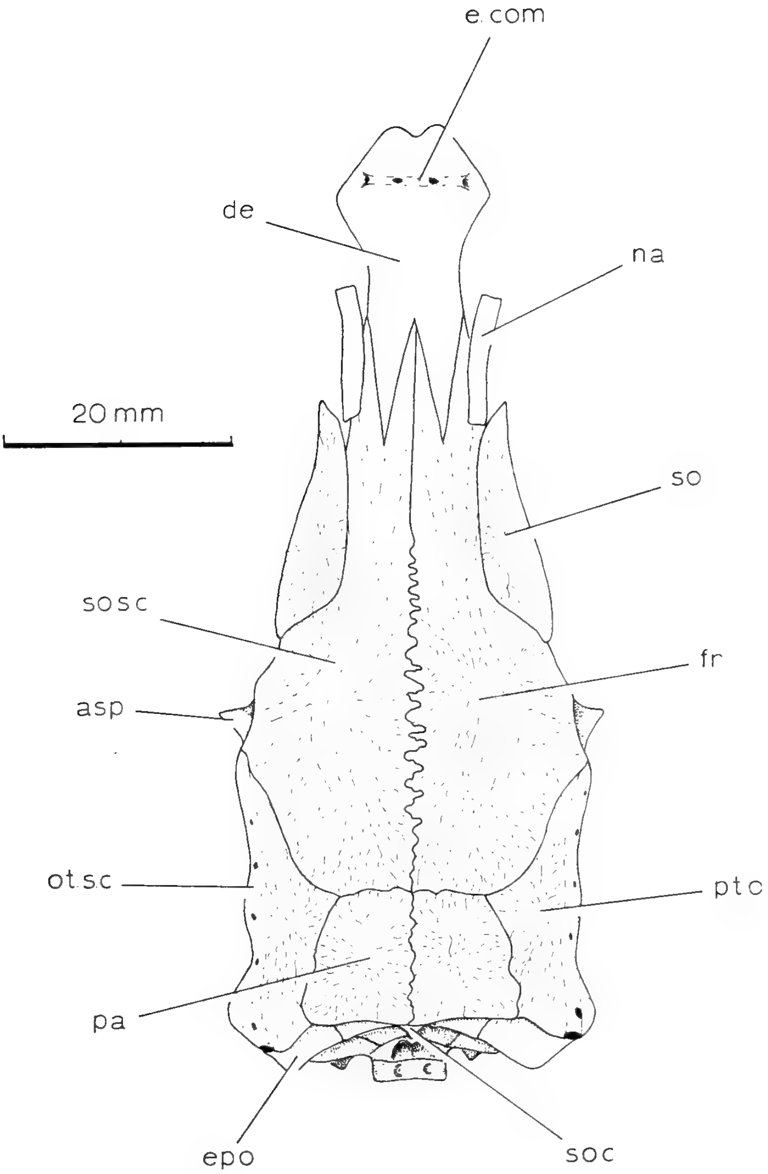

FIG. 46. *Osmeroides lewesiensis* (Mantell). Neurocranium in dorsal view. Composite of several B.M.N.H. specimens.

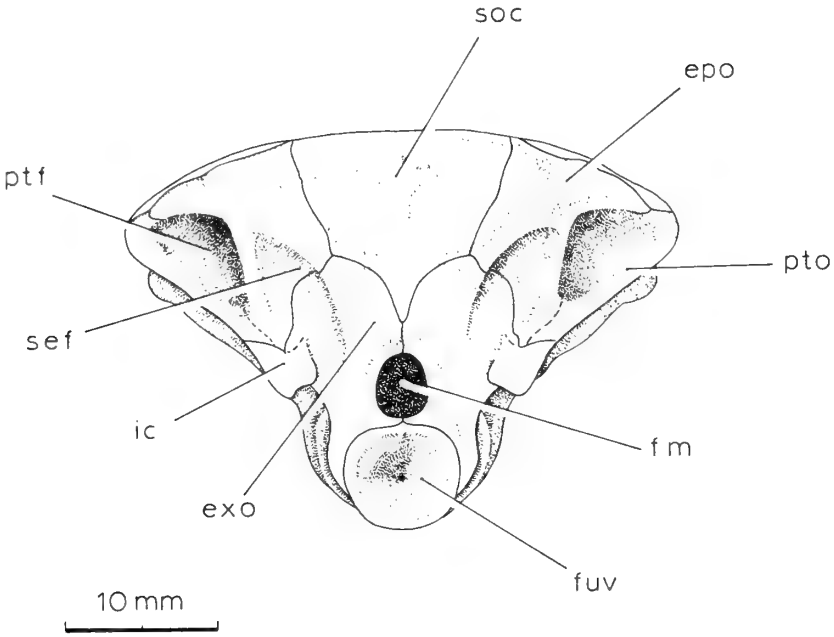

FIG. 47. *Osmeroides lewesiensis* (Mantell). Neurocranium in posterior view. Based on B.M.N.H. P.6456.

of the post-temporal fossa. The horizontal semicircular canal within the pterotic is indicated externally as an arch-shaped swelling immediately beneath the hyomandibular facet.

In posterior view the pterotic is seen to form part of the roof and the entire lateral border to the opening to the post-temporal fossa.

The epiotic forms part of the dorsal and the entire medial margin of the opening of the post-temporal fossa. Internally the epiotic forms a small portion of the medial wall of the fossa. Dorsally the epiotic is produced as a rounded process which receives the upper limb of the post-temporal. The posterior surface of the epiotic is deeply excavated, the excavation being continuous with that on the exoccipital and together forming a sub-epiotic fossa.

The supraoccipital is pentagonal in posterior view. Dorsally this bone separates the epiotics while ventrally it partially separates the exoccipitals. There is a very small supraoccipital crest. Internally the supraoccipital is continued forward as two antero-lateral wings which form much of the medial wall of the post-temporal fossa of either side.

The exoccipital meets its partner in the mid-line above and below the foramen magnum. Adjacent to the foramen magnum the exoccipital is produced posteriorly into a structure resembling a neural arch. The lateral face of the exoccipital forms part of the subtemporal fossa, the ventral edge of which is defined by a weak ridge on the exoccipital. Posteriorly, beneath the level of the intercalar, the exoccipital is pierced by the large, posteriorly directed vagus foramen. Smaller foramina adjacent to the vagus foramen may mark the point of exit of blood vessels and minor branches of the glossopharyngeal nerve. The main glossopharyngeal trunk left the cranial cavity through a forwardly directed foramen in the exoccipital, antero-ventral to the vagus foramen.

The intercalar forms a cap over the triradiate suture between the pterotic, epiotic and exoccipital. The intercalar is small but is produced posteriorly as a prominent knob for the attachment of the ventral limb of the post-temporal.

The basioccipital bears a facet on its posterior face which together with a facet on each exoccipital provides an attachment area for the first centrum ; this latter structure is functionally part of the neurocranium. Ventrally the basioccipital is grooved, but much of this groove is overlain by the posterior part of the parasphenoid. In transverse section the basioccipital is ' W' -shaped, the wings of the ' W ' enclosing the saccular recess of either side. The posterior region of the myodome roof is formed by the basioccipital. Laterally the wall of the basioccipital, together with adjacent regions of the exoccipital and prootic, is slightly inflated. This inflation, developed to a greater degree in *O. levis*, represents the lateral wall of the otolith chamber.

The prootic is the largest component of the lateral neurocranial wall. As seen in lateral view the bone is synchondrally united with the pterotic and autosphenotic dorsally and the exoccipital and basioccipital posteriorly, and syndesmotically joined with the parasphenoid ventrally. The anterior region of the subtemporal fossa and hyomandibular facet is formed by the prootic. A faint ridge upon the prootic continues that upon the exoccipital to form a ventral border to the subtemporal fossa. Beneath this ridge and close to the posterior margin of the prootic is a large jugular foramen which leads anteriorly to the pars jugularis. Posterior to the jugular foramen the path taken by the head vein is seen as a faint groove beneath the prootic-exoccipital ridge. A large hyomandibular foramen is situated antero-dorsally to the jugular foramen. A short canal links this foramen with the pars jugularis. The orbital artery entered the antero-ventral corner of the prootic, close to its union with the parasphenoid ascending wing, and passed upwards to pierce the floor of the pars jugularis. The external surface of the prootic is marked by a narrow ridge of bone running from above the orbital artery foramen to the level of the pars jugularis. This ridge, which represents a site of branchial muscle origin, is characteristic of many albuloids.

The anterior face of the prootic forms part of the posterior orbital wall. Dorsally this face contacts the autosphenotic, medially the pterosphenoid and ventrally the basisphenoid and parasphenoid. Two foramina pierce the anterior surface. The larger and more lateral is the anterior opening of the pars jugularis. The smaller foramen opens directly from the endocranial cavity and is the oculomotor foramen. From the dorsal margin of the anterior opening of the pars jugularis there is a groove running across the surface of the prootic and pterosphenoid. Within this groove lay the superficial ophthalmic branches of V and VII.

The medial wall of the pars jugularis is pierced by two foramina. The posterior of these is the facial foramen, and through this passed the hyomandibular trunk. The otic, superficial ophthalmic and buccal branches left the cranial cavity through

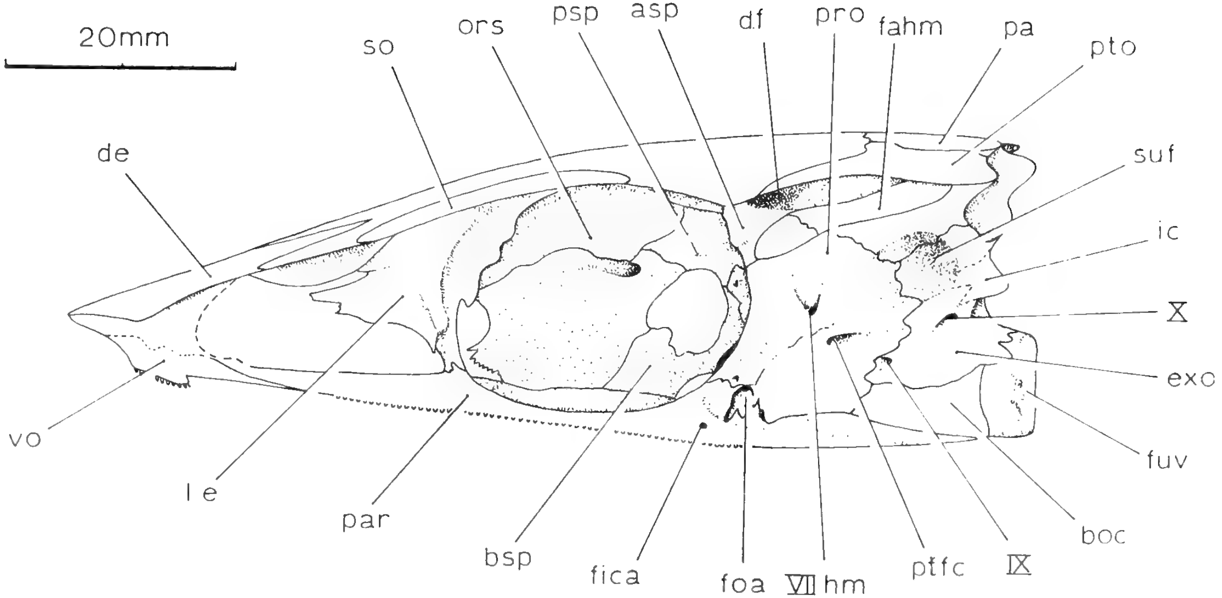

FIG. 48. *Osmeroides lewesiensis* (Mantell). Neurocranium in left lateral view. Based on B.M.N.H. P.6456, snout restored.

the trigeminal foramen. The latter foramen is situated anterior to the facial foramen and separated from it by a narrow prefacial commissure. The absence of a separate foramen for the profundus ciliaris leads one to suppose that it left the cranium with the trigeminal trunk. The medial surface of the prootic is marked by two shallow cups, adjacent to each of the foramina described above. These cups housed their respective ganglia and they are the only evidence of a defined pars ganglionaris.

Beneath the level of the pars jugularis the prootics are produced medially as a horizontal platform, the prootic bridge. The abducens nerve passed through the prootic bridge to the myodome.

The autosphenotic is tetrahedral in shape, the apex directed laterally and somewhat ventrally as a weakly developed autosphenotic spine. The otic ramus of VII pierced the anterior face of the autosphenotic. The posterior face of this bone forms the anterior wall of the deep dilatator fossa.

The pterosphenoid is of irregular shape. It contacts the basisphenoid ventrally and excludes the prootic from the optic foramen. Of the two foramina piercing the pterosphenoid beneath the superficial ophthalmic groove the anterior may be identified as having transmitted the trochlearis. The posterior is probably the point where the anterior cerebral vein left the cranial cavity.

The basisphenoid, when viewed anteriorly, is ' Y ' shaped, the wings of the ' Y ' contacting the prootic and pterosphenoid while the stem passes antero-ventrally, expanding in the sagittal plane as it does so. The ventral contact with the parasphenoid was probably by cartilage. From near the top of the basisphenoid stem a short prong of bone on either side passes ventro-laterally towards the myodome opening. The significance of this structure is unknown, but it appears to be part of the basisphenoid. It is also found in *Osmeroides levis*, *O. latifrons* and in *Tarpon* (p. 50).

In the dorsal half of the orbit the orbitosphenoid contacts the frontals dorsally and the pterosphenoids posteriorly. Although clearly paired dorsally, the orbitosphenoids unite ventrally where they pass into a completely ossified interorbital septum. The septum contacts the parasphenoid ventrally and the basisphenoid posteriorly. The olfactory tracts passed out of the orbitosphenoid anteriorly.

The lateral ethmoid forms the anterior wall of the orbit and the posterior and outer wall of the nasal capsule. It is composed of transverse and lateral faces which meet one another in a sharp ridge. This ridge is expanded laterally as a short spine. Beneath the spine the lateral ethmoid is sutured with the expanded parasphenoid. The transverse face of the lateral ethmoid meets the frontal dorsally. The unfinished nature of the anterior margin of the lateral face suggests that the bone passed into cartilage. Much of the ethmoid must have been cartilaginous, but a small area of spongy bone lying above the anterior part of the vomer represents a restricted mesethmoid.

The parasphenoid is stout and extends below most of the neurocranium. Anteriorly it widens in the region of the lateral ethmoid but posteriorly beneath the otic capsule it becomes narrower. The ascending wings of the parasphenoid are weakly developed. The internal carotid foramen is at the base of the ascending wing. Beneath the orbit the parasphenoid bears a large tooth plate which bifurcates anteriorly. The

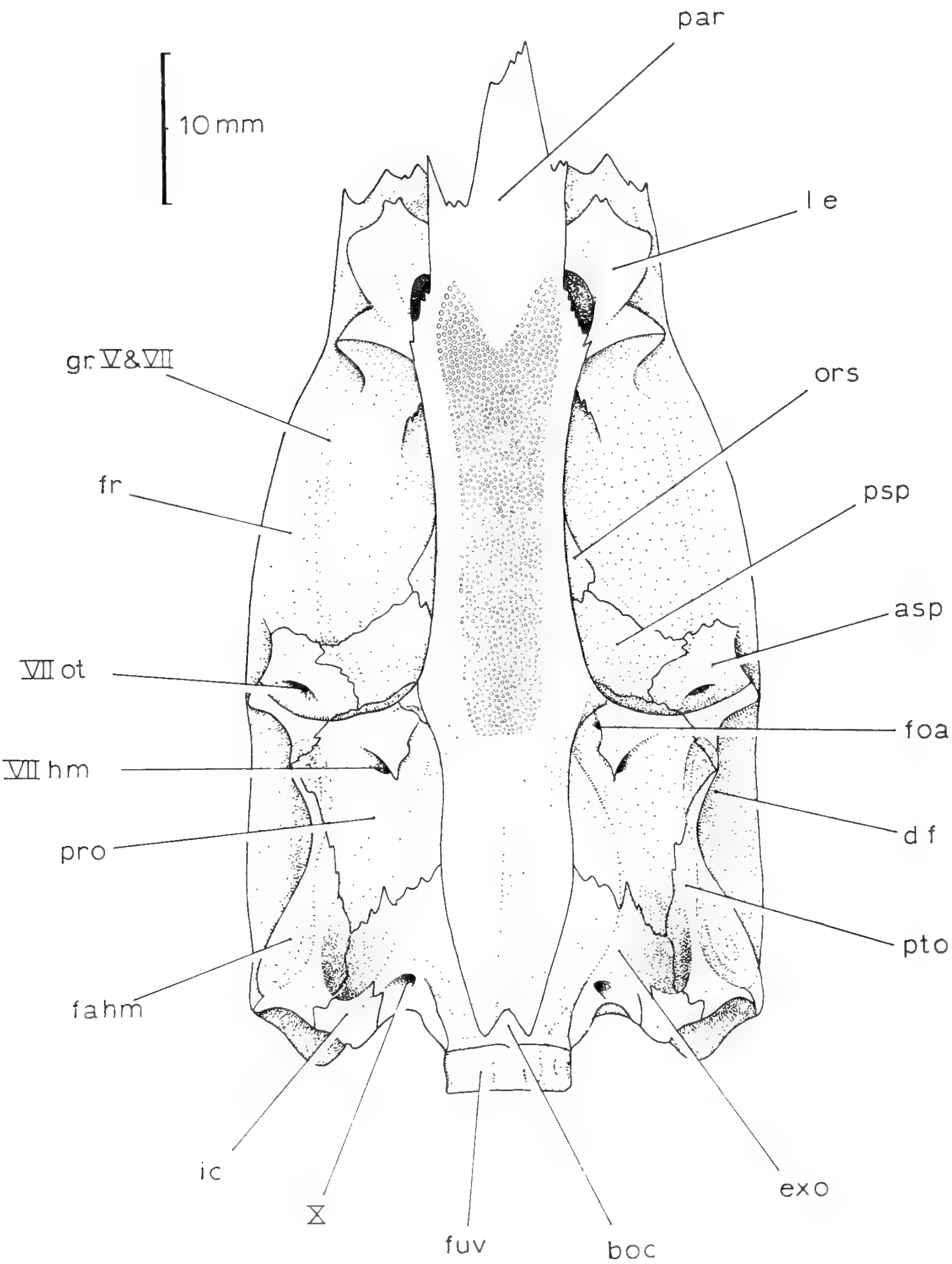

FIG. 49. *Osmeroides lewesiensis* (Mantell). Neurocranium in ventral view. Based on B.M.N.H. P.6456.

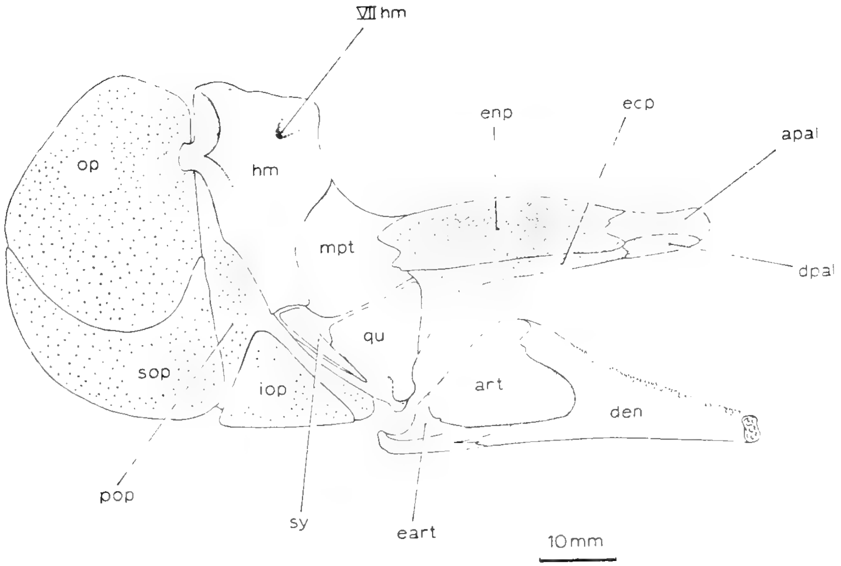

FIG. 50. *Osmeroides lewesiensis* (Mantell). Hyopalatine bones, opercular series (stippled) and mandible of the left side in medial view. Composite of several B.M.N.H. specimens.

plate bears numerous small villiform teeth of regular size. The vomer bears a large tooth plate which is partially divided into lateral halves ; the teeth are similar to those on the parasphenoid.

Hyopalatine bones. The hyopalatine bones are stout and firmly united to one another, forming a rigid roof to the buccal cavity.

The hyomandibular is broad and articulates with the neurocranium by a large head which is separable into swollen anterior and posterior regions. The lateral surface is marked by two ridges which originate from the articulatory regions and converge ventrally to form a single stout ridge running the length of the hyomandibular shaft. The medial surface of the hyomandibular is marked by a prominent groove which leads ventrally to a large foramen. This in turn leads to a canal opening beneath the opercular process on the posterior edge. The groove, foramen and canal mark the path of the hyomandibular trunk of VII and the efferent hyoidean artery. Anteriorly the head of the hyomandibular is produced as a thin wing which is partially covered ventrally by the metapterygoid.

The metapterygoid is large and irregularly shaped. Posteriorly and ventrally it lies in the vertical plane but antero-dorsally it twists horizontally to lie in continuity with the endopterygoid. Contact with the quadrate was mediated by cartilage, but with other bones union was syndesmotic. Dorsally, where it overlaps the hyomandibular, a cup-shaped depression is formed which received part of the levator arcus palatini muscle.

The quadrate is fan-shaped and has a deep ' V '-shaped notch which received the pointed end of the symplectic. The anterior border of the quadrate is thin and fits into a groove along the posterior margin of the ectopterygoid. This latter element is boomerang-shaped, with unequal limbs directed postero-ventrally and antero-dorsally. The anterior tip of the ectopterygoid fits into a small recess on the posterior aspect of the autopalatine. Small villiform and rounded teeth are borne along the entire buccal surface of the ectopterygoid. The anterior teeth are comparable in size to those on the parasphenoid, but posteriorly they become smaller.

The endopterygoid is large. Its convex buccal surface is covered with many small teeth. Posteriorly it is overlapped by the metapterygoid, anteriorly it contacts the autopalatine, while laterally it sutures with the ectopterygoid.

The autopalatine ends anteriorly in a transversely expanded condyle. This condyle contacts a process upon the maxilla laterally and presumably lay against the cartilaginous ethmoid medially. The dermopalatine is represented by a large oval tooth plate which bears similar teeth to those on the endopterygoid and anterior region of the ectopterygoid.

Dermal upper jaw. The upper jaw extends from the snout to the level of the quadrate/mandibular articulation. The ventral margin is convex. All bones are heavily ornamented with coarse rugae.

The premaxilla is tapered both anteriorly where it fits against the dermethmoid and posteriorly where it fits into a notch on the lateral face of the maxillary head. The premaxillae just meet in the mid-line, and form about 38 per cent of the upper jaw border. A broad band of many small villiform teeth is present on the premaxilla.

The maxilla ends anteriorly in a simple point where it lies against the ethmoid. A little further back the dorsal surface is raised in a small knob which articulated with the palatine head, probably through a biconcave sliver of cartilage, as in elopoids. The posterior end of the maxilla becomes slightly deeper where it is partially overlain by the supramaxillae. Teeth similar to those on the premaxilla occur along the entire oral margin of the maxilla. There are two supramaxillae set in tandem. The anterior supramaxilla is oval and overlain along much of its dorsal margin by a projection of the posterior element.

Mandible. The mandible is slightly longer than the upper jaw. The greatest depth of the mandible occurs at the coronoid process, situated at two-thirds of the mandibular length from the symphysis. The dentary forms the anterior two-thirds of the mandible. From the inturned symphysis the bone expands vertically and bears a narrow horizontal ledge along the ventral margin. Beneath this ledge is a line of 20–25 small pores set at regular intervals along the entire length of the dentary. The mandibular sensory canal ran within the articular posteriorly and the dentary anteriorly and communicated with the exterior via these pores. The posterior margin of the dentary has the shape of a lazy ' V ', the apex directed towards the symphysis. Medially the articular partially overlapped the dentary, there being a gap between these elements, the Meckelian fossa, which received the anterior extension of the A_w division of the adductor mandibulae. The oral surface of the dentary bears a broad band of villiform teeth.

The articular forms the posterior half of the coronoid process and the extreme outer edge of the articulatory cup. Ornamentation on the articular is confined to

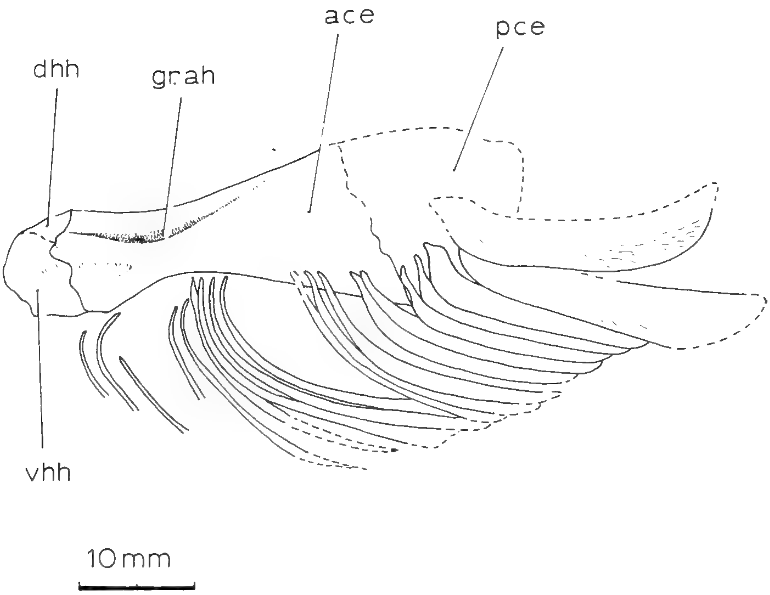

FIG. 51. *Osmeroides lewesiensis* (Mantell). Hyoid bar and branchiostegal rays of left side in lateral view. From B.M.N.H. P.5680.

the postero-lateral aspect. Upon the medial surface the articular bears a prominent ledge which is continued for a short distance on the dentary. The dorsal surface of this ledge is grooved and provided an attachment area for muscle fascia. In *O. levis* there is a small sesamoid articular resting on the ledge of the articular ; such an element was not seen in *O. lewesiensis*, but this is probably due to imperfection of the specimens. Much of the articulatory cup is formed by an endosteal articular which extends forward as a narrow splint overlying the articular ledge.

Circumorbital series. There are eight circumorbitals of which one, the supraorbital, is anamestic. The supraorbital is a long, narrow bone which lies, for the greater part of its length, in a narrow rebate on the frontal. The surface is ornamented in the same fashion as the frontal. The ventral end of the supraorbital contacts the small triangular antorbital.

The first infraorbital (lachrymal) is large with a rounded anterior border. The ventral margin overlaps the dorsal extent of the maxilla while dorsally there is a small rounded projection. The second infraorbital expands posteriorly where it meets the third in an oblique suture. The third, fourth and fifth infraorbitals are all wider than deep. A dermosphenotic was not seen in *O. lewesiensis*, but the gap left between the last infraorbital and the frontal suggests that one was present. No definite evidence of rostral ossicles could be found in any of the specimens examined.

Hyoid arch, branchiostegals and gular plate. Both the anterior and posterior ceratohyals are stout, the former being three times as long as the latter. The posterior ceratohyal shows a notch postero-dorsally which received the ventral end of the interhyal. The anterior ceratohyal is somewhat constricted mid-way along its length. Anteriorly the bone expands vertically and transversely. Of the two hypohyals, the lower is slightly the larger. The afferent hyoidean artery ran through both hypohyals and continued upon the lateral surface of the anterior ceratohyal in a prominent groove.

About 20 branchiostegals (range 18–21) are borne by the ceratohyal. Of these the first five or six (the first is taken as the upper or most posterior element) are broad and inserted upon the posterior ceratohyal. The anterior rays are slender and articulate with the outer face of the anterior ceratohyal. The gular plate is large, equal in length to two-thirds of the total mandibular length.

Cephalic sensory canal system. The supraorbital, otic, mandibular and ethmoid commissure sensory canals have been mentioned in connection with the bones through which they pass. These and the other cephalic sensory canals run deep within the cranial bones and the pores by which they open to the surface are often obscured by heavy ornamentation. The sensory canals do not show secondary branches, a point of distinction from most elopoids.

The infraorbital sensory canal ran close to the orbital margin of the infraorbitals. Anteriorly the canal terminates by a single pore at the antero-dorsal convexity of the lachrymal. A short, narrow antorbital canal runs through that bone and appears to end blindly. The only pores seen were those which opened within the lachrymal.

The preopercular sensory canal ran close to the anterior margin of the preoperculum, diverging slightly from its parallel course at the angle. The canal opened to the surface by 9–11 pores situated below the angle of the canal.

Within the supratemporal there is a canal which runs at the anterior margin and represents part of the supratemporal commissure. Since the supratemporals are widely separated from one another the central portion of the commissure must have lain in the dermis as in Recent albuloids. Laterally the commissure opens to the surface of the supratemporal by a single large pore. A canal linking the cephalic sensory system with the lateral line could not be seen.

Opercular series. All bones, except the interoperculum, are thick and ornamented by radiating rugae.

The operculum is trapezoidal in shape, with the longest edge situated anteriorly. The articulatory facet which fits the opercular process of the hyomandibular is near the top of this anterior edge. The facet is supported by a horizontal flange which also served as a point of insertion for the levator operculi musculature. Beneath this horizontal flange there is an upwardly directed foramen, but whether it penetrates the opercular bone (as does a similar foramen in *Scomber*, Allis 1903) is not known.

The suboperculum is large and continues the posterior border of the operculum. Anteriorly the suboperculum sends up a dorsally directed wing under the anterior margin of the operculum.

The interoperculum has the form of an equilateral triangle, with the anterior point lying adjacent to the articular, with which it was no doubt connected in life by ligaments. The interoperculum is distinctively short but deep. Laterally the interoperculum is largely overlain by the preoperculum.

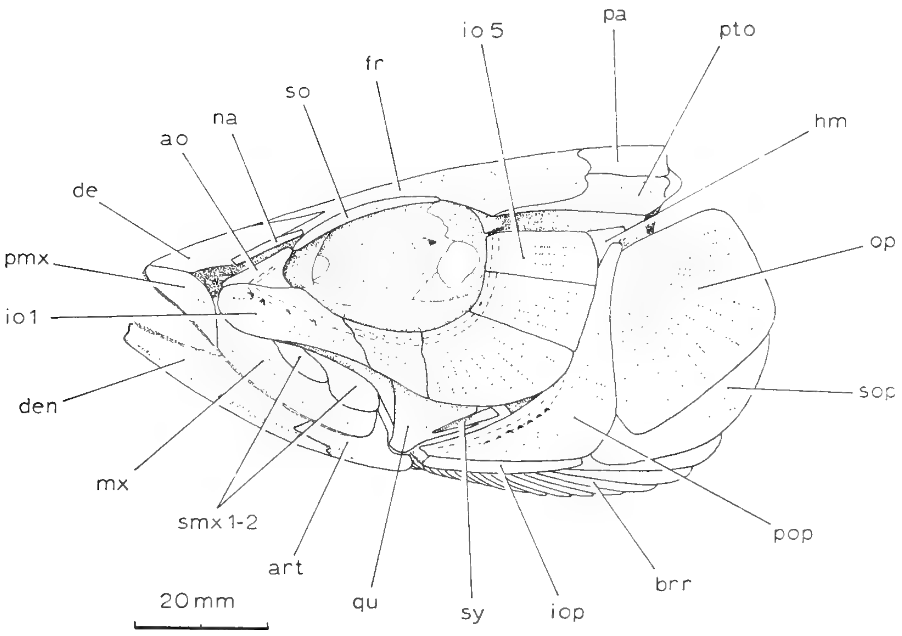

FIG. 52. *Osmeroides lewesiensis* (Mantell). Cranium in left lateral view. Composite of several B.M.N.H. specimens.

The preoperculum has two limbs, horizontal and vertical, the latter being the longer and lying closely against the hyomandibular. The anterior margin of the preoperculum is thickened, particularly in the angle, and forms, together with the hyomandibular, a prominent ridge for the origin of the adductor mandibulae. The preoperculum is relatively narrow throughout its length.

Pectoral girdle and fin. The supratemporal is triangular, ornamented with coarse rugae and lies tightly against the posterior margin of the pterotic. The supratemporal is separated from its partner as in all albuloids.

The post-temporal is relatively small, consisting essentially of two unequal limbs. The upper limb projects forward to overlie the epiotic process, to which it was no doubt connected by ligaments. The lower limb is very much smaller, both in length and diameter, and projects antero-ventrally to lie against the intercalar. Posteriorly the post-temporal overlies the top of the supracleithrum. The lateral line canal ran through the post-temporal and continued within the dorsal part of the supracleithrum. This latter element curves ventrally and overlies the dorsal part of the cleithrum. Dorsally and ventrally the supracleithrum ends in rounded margins.

The cleithrum is by far the largest element in the girdle, extending from the posterior angle of the operculum to the medial surface of the interoperculum. The anterior margin of the cleithrum is turned medially and thus presents a broad face for the attachment of the sternohyoideus musculature. The posterior margin of the cleithrum curves postero-ventrally to just above the fin insertion. At this point the border turns sharply antero-ventrally. Anteriorly and ventrally the tip of the cleithrum is inwardly curved and meets its partner in the mid-line.

Specimen B.M.N.H. P.6456 shows fragmentary remains of the endochondral elements. The scapula fails to enclose the scapular foramen, the outer (upper) margin of this foramen being formed by the cleithrum. A notch in the posterior border of the scapula marks the position of insertion of the outermost fin-ray. The coracoid is incompletely known. Posteriorly this element appears to contact the scapula laterally and mesocoracoid dorsally. Anteriorly it is in contact with the cleithrum over a very small area. Much of the coracoid is separated from the cleithrum by a large fenestra. The mesocoracoid forms the mesocoracoid arch. The bone is narrow in its centre, but dorsally it expands to spread over the medial surface of the cleithrum, while ventrally it was in synchondral union with the scapula and coracoid.

There are approximately 15 pectoral fin-rays (as with other fins the exact number cannot be ascertained) of which the outermost is distinctive in having a swollen base. All rays are articulated and, except the first, are branched. A pectoral splint is present.

Pelvic girdle and fin. The pelvic fin, which originates mid-way between the snout and caudal peduncle, is supported by a simple pelvic bone. Each pelvic bone is triangular in shape and thickened posteriorly. The surface marking of the posterior face suggests that it was covered by cartilage. The number and size of the pelvic fin-rays is not known, Woodward (1908) stated that 11 rays were present but this could not be verified.

Vertebral column. Virtually nothing is known of the vertebral column. Woodward (1901) quotes a rather wide range of 50–70 vertebrae, and this is all that may be suggested with known material. The majority of the centra are as deep as long and are marked laterally by a few longitudinal grooves. Exceptions to this general form are the last few centra which are slightly longer than deep.

The neural and haemal spines are stout and the arches are lodged in depressions upon the centra. The abdominal centra bear autogenous parapophyses with which the pleural ribs articulate. Dorsal (i.e. epineural) intermuscular bones are present in the abdominal but apparently not in the caudal region. The absence of intermusculars in the caudal region may be apparent rather than real since in many Recent teleosts the posterior intermusculars have no firm attachments to the vertebral column and are often dislodged when the flesh is removed.

Modification at the posterior end of the column in support of the caudal fin-rays is dealt with in the description of the caudal fin.

Median fins. The origin of the dorsal fin occurs mid-way between the snout and the caudal peduncle. The base length of the fin is slightly greater than its height. Woodward (1901 : fig. 2) illustrates 22 fin-rays but the specimens show a lower count, 18–19, of which the first three are unbranched and the first is not jointed. The fifth ray is the longest of the series.

The anal fin originates nearer to the caudal peduncle than to the pelvic fins. The base length is almost equal to the length of the longest ray which is the first branched and the fourth in a series of 14. The anterior two rays are not jointed.

Very few specimens of *O. lewesiensis* show the dermal rays of the caudal fin; none shows a complete series and thus the number, nature, length and distribution are unknown. The following description of the caudal skeleton is based on B.M.N.H. 49894.

The fin-rays are supported by structures associated with four preural and two ural centra. The latter are distinguished from those anteriorly by being unornamented, upturned and longer than they are deep.

The haemal arches borne by the first four preural centra are firmly united, although not fused, with the centra. The haemal spines remain broad throughout their length and are thickened along their posterior margins. The anterior margin is produced as a thin wing which lies against the preceding spine. Near to the base of the spine the anterior margin is notched for the passage of the segmental artery.

The third and fourth preural centra bear full length neural spines which converge distally. The second preural centrum bears a neural arch and a half length spine, while the first preural bears only a neural arch, the outline of which is difficult to see. All neural arch elements are autogenous.

The hypural series forms a complete fan. Two lower hypurals are borne by the first ural centrum. The lowermost or first hypural is by far the larger of the two and is fan-shaped, in contrast to the parallel-sided second element. The bases of these hypurals are slightly constricted and produced into rounded heads which fit in weakly defined cup-shaped depressions on the supporting centrum.

Three upper hypurals may be seen (though it is very likely that there was a fourth in the series representing the 'hypurale minimum' of Monod 1967). The third hypural, the lowermost member of the upper series, is large and fan-shaped. It is divisible into a thickened upper and a thin lower portion. The fourth hypural is considerably narrower, but similar to its ventral neighbour in articulating with the second ural centrum.

There are four uroneural elements. The first is expanded proximally and covers the dorso-lateral surface of the first and second preural centra. The second uroneural, which in the specimen figured (Text-fig. 53) is displaced posteriorly, is slightly smaller and lies in a groove on the posterior face of the first uroneural. The third lies in conformity with the second but the fourth appears to have been displaced posteriorly. The nature of this fourth element is in question. Its size and shape would suggest that it represents a urodermal, but its position within the fin-rays, not superficial to them, and the nature of the bone surface are features of a uroneural. This structure is interpreted as being a fourth uroneural.

Between the first uroneural and the second preural neural spine there are three epurals. The posterior epural is the largest. The anterior epural is markedly curved but it is not clear how much of this curvature is due to the distortion which has obviously taken place.

The base of the inner ray of the upper lobe shows a marked basal expansion as in many lower teleosts. A caudal scute was present both above and below the caudal peduncle.

Squamation. A lateral line scale count cannot be made. The type specimen exhibits 38 scales to the level of the pelvic fin insertion. If the pelvic fin origin be

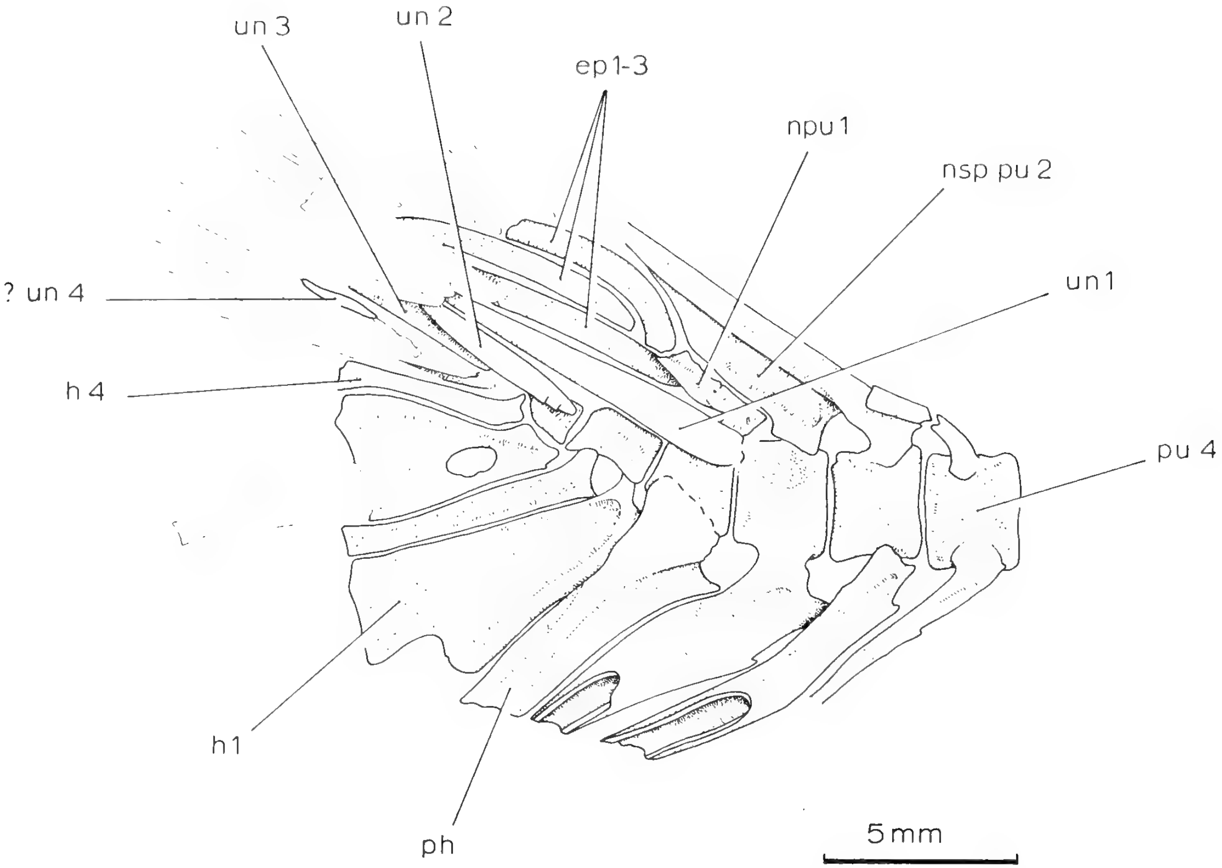

FIG. 53. *Osmeroides lewesiensis* (Mantell). Caudal skeleton in right lateral view. From B.M.N.H. 49894.

taken as representing the mid-body level then the total lateral line count must have been about 80 (Woodward 1901 : fig. 2, indicates 87). The transverse count is 7/6 at both the occiput and the dorsal fin.

The scales have a characteristic shape and together with those of *O. levis* are distinctive among remains of the English Chalk fish fauna. Each scale is large, angular anteriorly but smoothly rounded posteriorly. The exposed portion is marked by fine tuberculations set in an apparently irregular fashion. The covered portion bears many smaller tuberculations and these are set in a radial pattern. Fine circuli are arranged concentrically around a central nucleus. The majority of the anterior body scales are marked by 3–8 (mode 5) radii which produce a scalloped margin anteriorly. Towards the tail the scales appear more rounded and do not bear radii. Lateral line scales are marked by a longitudinal ridge which terminates as a notch on the posterior margin of the scale.

Osmeroides levis Woodward

(Text-fig. 54)

1895 ***Aulolepis typus*** Agassiz ; Woodward : 660, pl. 43, figs. 2, 3, 5 (*errore*).
1900 *Osmeroides* sp. ; Woodward : 325.
1901 *Osmeroides levis* Woodward : 15.
1907 *Osmeroides levis* Woodward; Woodward : 118, pl. 23, figs. 9–11.

DIAGNOSIS (emended). *Osmeroides* reaching a maximum length of 200 mm. Length of cranium not exceeding twice its maximum width at the sphenotic region. Parietals as long as wide. Dermal skull bones smooth, ornamented only by weakly developed radiating ridges. Interorbital septum partially ossified. Parasphenoid ending beneath mid-otic region. Quadrate/mandibular articulation beneath middle of orbit. Branchiostegal rays smooth, exact number not known but not less than 15. Vertebrae, dorsal fin and scales as in the type-species.

HOLOTYPE. B.M.N.H. P.5681, from the Upper Cenomanian (*Holaster subglobosus* zone) of Burham, Kent, England.

MATERIAL. The holotype and the following B.M.N.H. specimens; 49903 (paratype), P.1854 (part and counterpart), P.36204. The last specimen was prepared in acid by Dr C. Patterson. All specimens are from the Upper Cenomanian of S.E. England.

REMARKS. *O. levis* is both rarer and more restricted in time than the type-species. Although the specimens are not accompanied by horizon data the matrix in which they are embedded is easily identifiable as having the lithology of the *Holaster subglobosus* zone, and is therefore of Upper Cenomanian age.

Other than the cranium very little is known of the anatomy. However, sufficient evidence remains to indicate that *O. levis* is very closely related to the type-species.

Woodward (1907) noted the following differences between *O. levis* and the type-species. The head and opercular apparatus occupy one-third of the standard length (taken in this instance as the distance between the snout and the caudal peduncle), whereas the head and opercular apparatus are relatively shorter in the type-species.

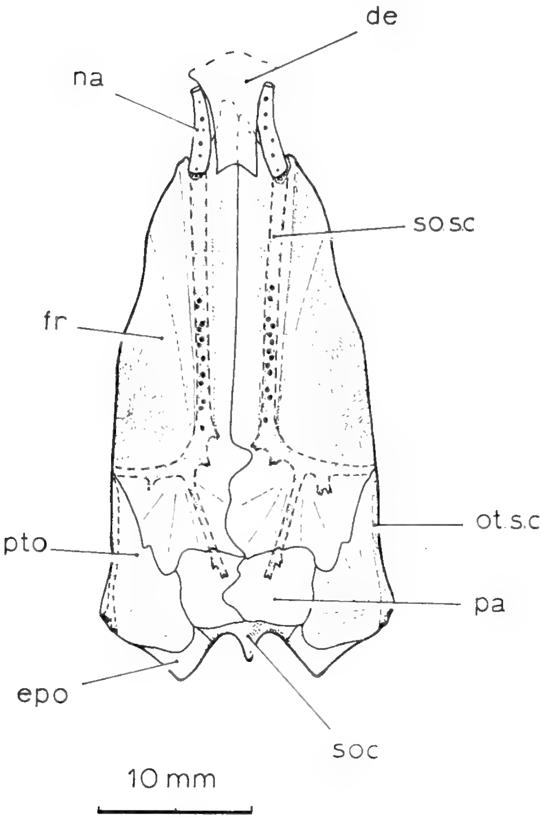

FIG. 54. *Osmeroides levis* Woodward. Neurocranium in dorsal view. Based on B.M.N.H. P.5681, P.1854 and 49903.

The cranial roof is shorter in proportion to its width than in the type-species and the parietal bones are shorter than long. Perhaps the most easily recognizable difference noted by Woodward concerns the ornamentation of the skull roofing bones, those of *O. levis* being smooth except for a small patch of rugose ornamentation on the frontal bones above the orbit, whereas the roofing bones of the type-species are uniformly ornamented from the mid-orbital region posteriorly.

In addition to the above differences several others may be mentioned. The dermethmoid of *O. levis* is considerably shorter than that of the type-species and this is related to the preorbital length which is less in *O. levis*.

The parasphenoid of *O. levis* is relatively narrow and terminates beneath the middle of the otic region of the neurocranium, contrasting with the very broad, long parasphenoid of *O. lewesiensis*. In both species the parasphenoid bears a patch of very small, rounded teeth. The size of the parasphenoid has resulted in other differences between the two species. The parasphenoid rests against the lateral ethmoid in both, but in *O. lewesiensis* there is a sutural connection between these elements, whereas in *O. levis* there is an interspace. The interorbital septum is not completely ossified in *O. levis* in contrast to the well-ossified septum in *O. lewesiensis*. Posteriorly the myodome is open in *O. levis* whereas in the type-species it is closed.

Apart from the differences noted above, the neurocranium is very like that of the type-species. Woodward (1907 : 118) described much of the cranial anatomy other than the neurocranium, and the following notes, based upon an examination of B.M.N.H. P.36240, are intended to supplement that work.

Hyopalatine bones. The hyomandibular tapers from a broad undivided head to a vertically directed shaft, unlike the forwardly directed shaft of the type-species. The opercular process is large, rounded and bears a stout horizontal ridge upon its medial surface. This ridge provided a point of insertion for the levator opercularis muscle. Laterally the shaft of the hyomandibular bears a stout ridge behind which there is a well-marked groove. Two foramina open into the groove from a single intraosseous canal, the upper representing the point of exit of the hyoidean nerve, the lower the mandibular nerve. The nerves continued within the hyomandibular groove. As in the type-species, the anterior margin of the hyomandibular is produced into a thin wing which is partly overlain by the metapterygoid.

The remainder of the hyopalatine series is very similar to that of *O. lewesiensis*, the only notable difference being that the quadrate is deeper than long in *O. levis*, which is the converse of the type-species.

The hyoid arch and branchiostegal rays. The interhyal was not identified in any specimen, although its presence is indicated by a notch upon the dorsal surface of the posterior ceratohyal. The posterior ceratohyal is approximately triangular, smooth upon the medial surface, but marked laterally by two depressions separated by an antero-ventrally inclined ridge. The anterior ceratohyal is elongate and waisted in the anterior third. It is deepest posteriorly where it contacted the posterior ceratohyal through a narrow band of cartilage. A prominent groove close to the dorsal margin of the lateral surface of the anterior ceratohyal marks the path of the afferent hyoidean artery. Ventrally the anterior ceratohyal shows a groove flanked medially by a notched ledge. Each of these notches marks the point of insertion of a branchiostegal ray suggesting that not less than five branchiostegals were attached along this margin.

There were two hypohyals, although only the upper is known. This is cuboid in shape and was separated from both the ceratohyal and lower hypohyal by cartilage. The groove for the afferent hyoidean artery runs along the dorsal surface of the upper hypohyal. In the type species the artery runs through the upper hypohyal.

The median urohyal is ' T '-shaped in cross-section. Anteriorly the horizontal lamina of bone is constricted before becoming expanded into two antero-laterally directed prongs. The median vertical flange of bone is thin, but its posterior extent is not known.

Not less than 15 branchiostegal rays are present. The anterior branchiostegals are narrow but the posterior rays are broad and marked by a stout ridge which runs down the centre of their length.

Gill arches. Very little is known of the branchial arches in this or the type-species. The basihyal and basibranchials were covered by two large tooth plates, the basihyal plate and an elongate basibranchial plate representing the compound plate associated with the first three basibranchials. The teeth borne by these plates are small, set in shallow sockets and range in shape from conical to hemispherical. On the basibranchial plate the teeth situated anteriorly are slightly larger than those posteriorly.

The cerato- and epibranchials are long, thin, and bear a deep groove upon the lateral face for the branchial arteries. The medial surface of these elements is smooth and the associated tooth plates lay free in the dermis. The tooth plates are oval in shape and bear villiform teeth. Somewhat larger tooth plates may be identified as infrapharyngobrancial tooth plates (upper pharyngeals of Nelson 1969a). The teeth borne by the upper pharyngeals are smaller than those on the basibranchial tooth plates.

Postcranial skeleton. What little is known of the postcranial skeleton is very like *O. lewesiensis.* The squamation is similar to that of the type-species but, as may be expected in a smaller fish, the scales show much less ornamentation.

Osmeroides latifrons Woodward

(Text-figs. 55–59)

1907 *Osmeroides latifrons* Woodward : 119, pl. 24, figs. 1, 2, 3.

Diagnosis (emended). Species known only from the cranium and anterior part of trunk. Length of cranial roof less than twice the maximum width, at the sphenotic level. Parietals broader than long. Frontals becoming narrow above lateral ethmoids. Dermal cranial bones smooth, marked only by fine radiating growth lines. Interorbital septum absent or membranous. Parasphenoid reaching rear of neurocranium. Quadrate/mandibular articulation beneath lateral ethmoid. Branchiostegal rays less than 15 in number. Scales large, exposed area marked by a fine reticulation of rugae. Anterior field of scales without radii.

Holotype. B.M.N.H. P.10465, exhibiting skull roof, from the Upper Cenomanian of Kent, S.E. England.

Material. In addition to the type, B.M.N.H. specimens P.5679, P.9699, P.10466 and P.11190 were examined. The last-mentioned specimen was prepared in acetic acid. All specimens are from the Upper Cenomanian of Kent, S.E. England.

This species is known only by imperfect cranial remains and the anterior region of the trunk. The account of the cranium is based mainly on B.M.N.H. P.11190.

Description. *Osmeroides latifrons* differs considerably from other species of *Osmeroides.* Many of the observable differences are features in which *O. latifrons* resembles the Albulidae and Pterothrissidae. However, a basic similarity in neurocranial structure and the retention of several primitive features justify the inclusion of this form within the genus *Osmeroides.* The description given below is designed to illustrate the differences between *O. latifrons* and the type-species, *O. lewesiensis.*

Neurocranium. The cranial bones are unornamented, except for a few lines of growth on the frontal, infraorbitals and operculum. Comparing the neurocranial

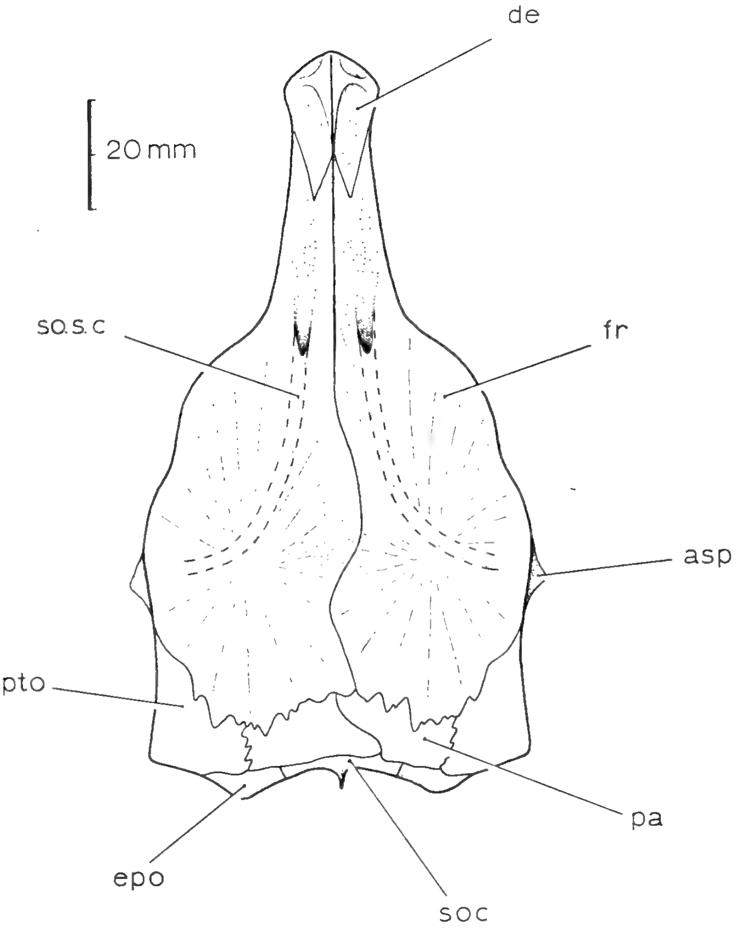

Fig. 55. *Osmeroides latifrons* Woodward. Neurocranium in dorsal view. Based on B.M.N.H. P.10465.

views (Text-figs. 55 and 46, 56 and 47, 57 and 48), the differences in proportion are obvious. The significant features of the neurocranial roof are : the narrow, slightly elongated snout, the broad otic region, the irregular shape of the parietals and the long dermethmoid. The dermethmoid shows a prominent median ridge which is continued posteriorly on the frontals. At the anterior end of the dermethmoid there are inclined struts of bone connecting the horizontal and vertical portions of this element ; in this the dermethmoid resembles that of albulid and pterothrissid fishes. The frontal of *O. lewesiensis* is flat throughout but in *O. latifrons* the centre of ossification is raised and there is a shallow trough developed anteriorly, features seen in the albulids and, to a lesser degree, in the pterothrissids.

The supraoccipital of *O. latifrons* is relatively small and there is a small, deep depression on either side of the weakly developed crest. The sub-epiotic fossa is

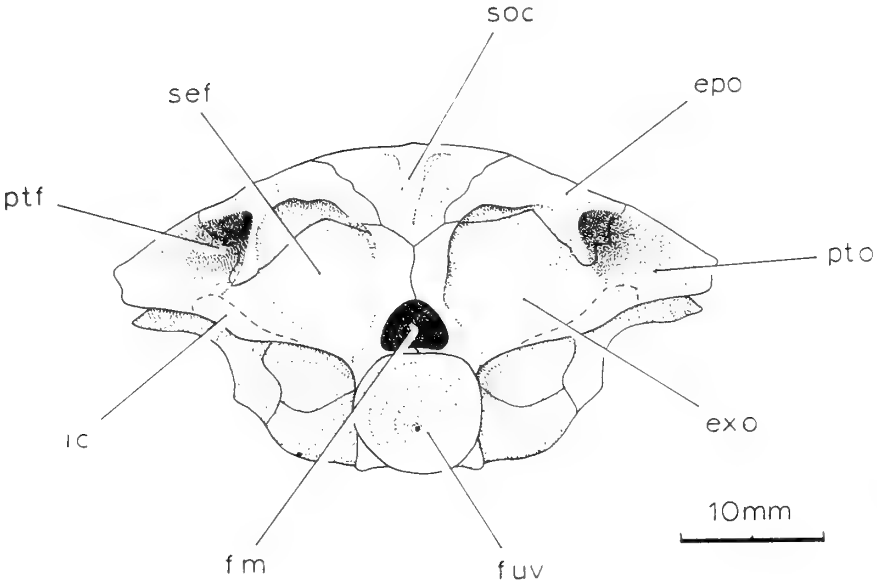

FIG. 56. *Osmeroides latifrons* Woodward. Neurocranium in posterior view. This and Text-figs. 57 and 58 from B.M.N.H. P.11190.

very large and the ridge which forms the medial margin in all *Osmeroides* species is particularly well developed here. The intercalar was not seen but the surface markings on the exoccipital and pterotic suggest that it was of limited size (Text-figs. 56, 57 and 58).

The lateral surface of the neurocranium shows a large otic bulla and a deep subtemporal fossa. Both of these structures are developed to a greater degree than in the type-species. Indeed, the subtemporal fossa is so deep that it severely restricts the lumen of the post-temporal fossa. Also seen upon the lateral face of the prootic is a prominent ridge of bone which passes antero-ventrally from the level of the pars jugularis. This ridge, which provided a site of origin for branchial musculature, is present but less pronounced in other species of *Osmeroides*.

The trigemino-facialis region is basically similar to that of the type-species, but there are two small differences. Firstly, the profundus ciliaris of *O. latifrons* leaves the cranial cavity by a separate foramen, whereas in *O. lewesiensis* that nerve ran out from the cranial cavity with the trigeminal nerve. The second difference concerns the path taken by the orbital artery. The condition in *O. lewesiensis* has been described (p. 99) and is quite typical of elopiforms. In *O. latifrons* (as represented by B.M.N.H. P.11190) an unusual condition existed. The orbital artery pierced the lateral face of the prootic and turned antero-dorsally to pass into the orbit immediately beneath a small bridge of bone, without taking its usual path through the pars jugularis. The path of the orbital artery presumably resulted in the efferent hyoidean branch looping back into the pars jugularis before running out of the prootic with the hyomandibular ramus of the facial. Since only one suitable specimen of *O. latifrons* was available it is not certain if the unusual disposition of the orbital artery is normal for this species or merely an individual variant.

Within the orbit *O. latifrons* differs from the type-species in the membranous interorbital septum and the small basisphenoid stem, although, as in *O. lewesiensis*, there are two posteriorly directed prongs arising from the posterior margin of the stem. The parasphenoid of *O. latifrons* is proportionally wider throughout, particularly beneath the otic region. The parasphenoid tooth patch is as extensive as in the type-species but the teeth are slightly different. The parasphenoid teeth of *O. latifrons* are of irregular size and vary in shape from small, villiform teeth to larger hemispherical teeth. The teeth become larger posteriorly and those in the centre are larger than the marginal teeth.

Hyopalatine bones. The quadrate/mandibular articulation lies beneath the lateral ethmoid, further forward than in the type-species. A distinctive feature of the hyomandibular is the thin bone forming the head; otherwise there is agreement in form with *O. lewesiensis.* The metapterygoid is imperfectly preserved dorsally, but it probably reached the antero-dorsal point of the hyomandibular and resulted in the presence of a hyomandibular-metapterygoid foramen as in albulids and pterothrissids. The lateral surface of the metapterygoid is marked by a prominent ridge, present in other species of *Osmeroides*, which provided an anchorage for a superficial division of the levator arcus palatini musculature. The quadrate, although of normal shape, is positioned so that the posterior margin lies almost horizontally. There is a considerable gap between the ventral end of the hyomandibular and the quadrate. This gap was presumably bridged by the symplectic. The symplectic was not seen but the impressions left upon the quadrate suggest that it was somewhat flattened, as in *Albula*. The metapterygoid contributes to the symplectic support. The ectopterygoid is almost as wide as the endopterygoid but

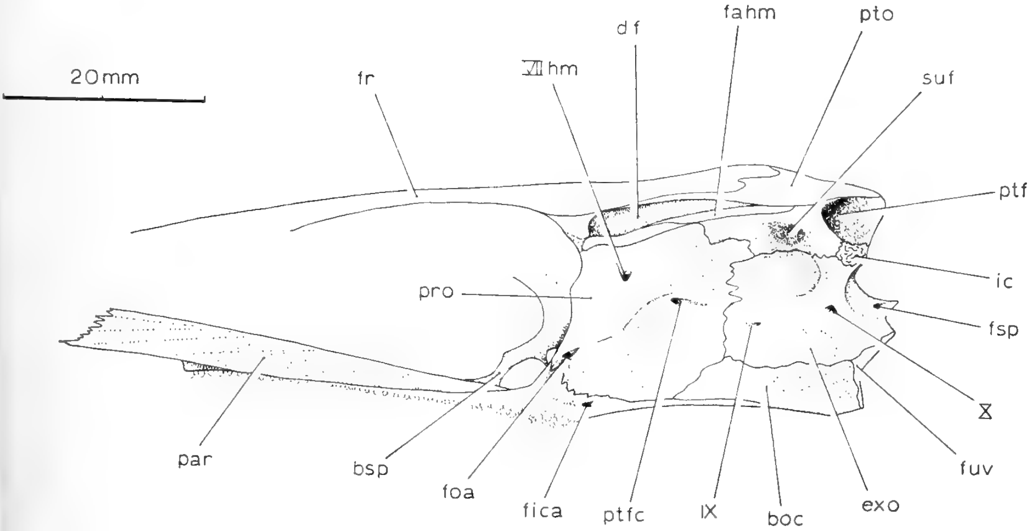

FIG. 57. *Osmeroides latifrons* Woodward. Neurocranium in left lateral view.

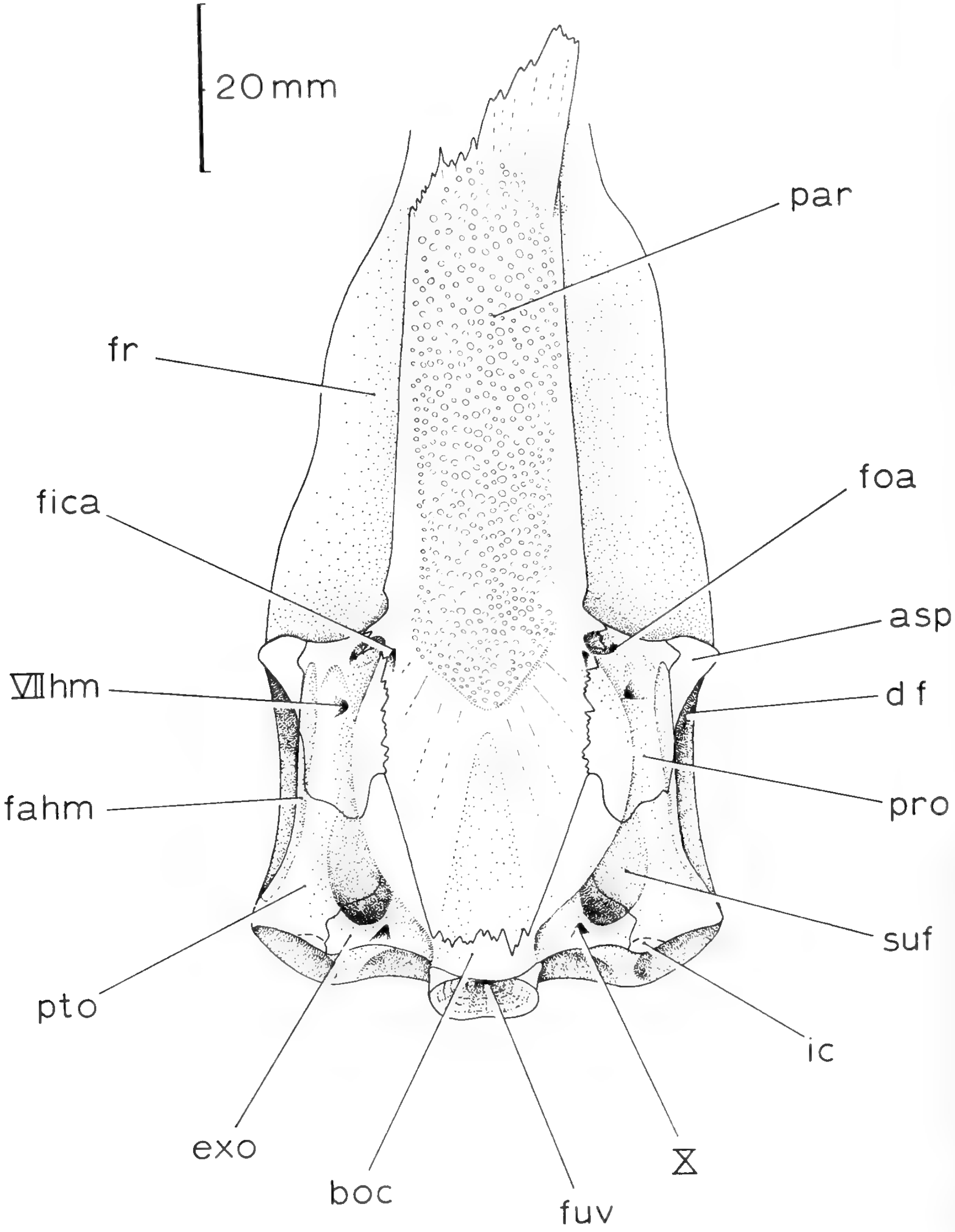

FIG. 58. *Osmeroides latifrons* Woodward. Neurocranium in ventral view.

unlike the latter is vertical. The dorsal margin of the lateral face of the ectopterygoid is produced as a small crest. The teeth borne by the ectopterygoid and endopterygoid form a single large patch. Unlike those in *O. lewesiensis*, the teeth in this patch vary considerably in size and shape. Those situated medially resemble the larger parasphenoid teeth. Those found laterally are similar to the villiform teeth seen in the type-species. The anterior end of the hyopalatine series is not known.

Mandible. The mandible is short, turned inwards markedly at the symphysis and with a posteriorly situated coronoid process. Ventrally the dentary is marked by a deep groove which runs parallel to the inflected margin, and carried the sensory canal. Posteriorly the mandibular sensory canal ran through the articular. The oral surface of the dentary bears a broad band of teeth. Each tooth is pointed and curves inwards distally like those of *O. levis* but unlike the villiform teeth of *O. lewesiensis*. The articulatory facet is formed mainly by the endosteal articular which is relatively larger than that element in the type-species.

Circumorbital series. The anterior half of the first and the third, fourth and fifth infraorbitals are the only elements of this series known. Unlike those of the type-species, all bones are thin and marked only by growth lines. The first infraorbital shows a rounded anterior margin and is without the small dorsal prominence seen in *O. lewesiensis*. The surface of the first infraorbital is marked by concentric growth lines and in the dorsal half there is a thin ledge which protected the sensory canal. The third, fourth and fifth infraorbitals form the posterior border of the orbit. These elements are narrower than those of *O. lewesiensis*, leaving more of the cheek region exposed.

Hyoid arch and branchiostegal rays. Both anterior and posterior ceratohyals are short and deep, contrasting with those of the type-species. The posterior ceratohyal carried five branchiostegals and at least six are attached to the anterior ceratohyal. All branchiostegals are smooth but otherwise they resemble those of *O. lewesiensis*.

Cephalic sensory canal system. The sensory canal system is more open than in *O. lewesiensis*. The supraorbital canal ran within the frontal from the level of the autosphenotic to open onto the surface of the frontal at the level of the lateral ethmoid. Anterior to this the canal must have lain in the frontal trough. The infraorbital sensory canal of *O. latifrons* is relatively larger than that of *O. lewesiensis* and, unlike that of the latter species, is situated at the orbital margin. Within the third infraorbital the canal opens to the surface by large pores, separated from one another by narrow bony struts. On the first infraorbital the canal must have been open ventrally, the only protection being afforded by a narrow ledge of bone. The mandibular sensory canal was similarly open, lying as it did in a large groove. The only point at which the canal passes through bone is at the extreme postero-ventral angle of the articular. The preopercular sensory canal ran within an intramural canal in the dorsal half of the preoperculum. At the level of the fourth infraorbital the canal emerged to the surface and continued its path beneath a narrow shelf.

Opercular series. The preoperculum is large and reaches well forward. The dorsal end of this element is narrow and truncated. Anteriorly the bone is rounded. The operculum differs in shape from that of the type-species. The anterior margin is almost straight while the posterior border curves backwards and downwards to near

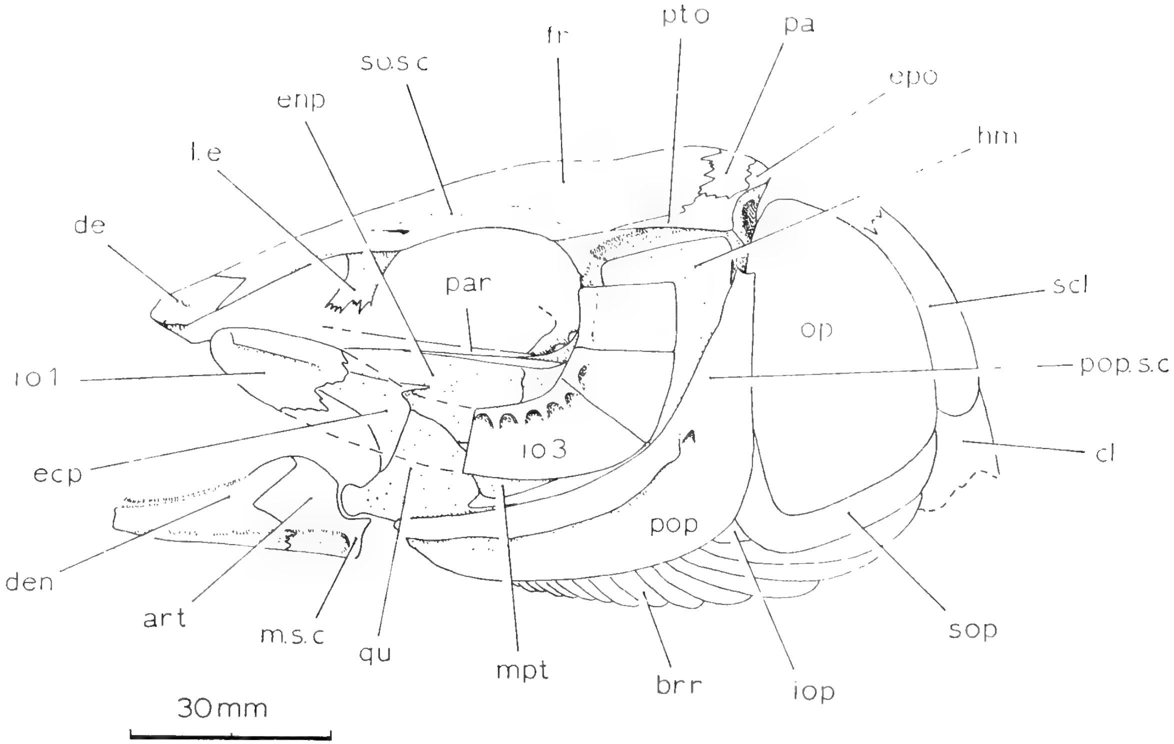

FIG. 59. *Osmeroides latifrons* Woodward. Cranium in left lateral view. Composite from B.M.N.H. P.10465, P.9699, P.10466 and P.11190.

the ventral end of the bone, where it curves sharply forwards resulting in an oblique ventral border. The suboperculum and interoperculum have the same form as in *O. lewesiensis.*

Squamation. Only a few of the anterior scales are known. The scales are thinner than in the type-species although of the same relative size. Each scale is nearly circular. The anterior field is marked by random fine granulations. In the dorsal and ventral fields the granulations become defined as circuli while in the posterior field they form a network of rugae and thus differ from those in *O. lewesiensis* which are set in radiating fashion. The scales of *O. latifrons* are without anterior radii and the anterior margin is complete ; a few of the anterior body scales of the type-species are also without radii. The lateral line scales may be identified by a small notch in the posterior margin, as in *O. lewesiensis.*

AFFINITIES OF *Osmeroides latifrons*. *Osmeroides latifrons* is an advanced species of the genus. Many features of *O. latifrons* are interpreted as the initiation of trends which are characteristic of albulids and pterothrissids. For instance, the cephalic sensory canals of *O. latifrons* are considerably more open than those of *O. lewesiensis* or *O. levis,* but are never cavernous as in the Albulidae and Pterothrissidae. Intermediate conditions of other characters are seen in the snout, hyopalatine series and the dentition, and are discussed in relation to the evolution of the Albuloidei (pp. 202–210). Despite certain resemblances to the Albulidae and Pterothrissidae, *O. latifrons* retains primitive characters of the Osmeroididae such as the terminal mouth, the incorporation of the first centrum into the neurocranium, the unexpanded ectopterygoid process, the presence of many ectopterygoid teeth and the unspecialized dentition, particularly that associated with the gill arches. In all, the known osteological features of *O. latifrons* show a closer resemblance to other species of *Osmeroides* than to any other albuloid genus. Those points in which *O. latifrons* differs from *O. lewesiensis* and *O. levis* concern degree of development rather than absolute difference and it is therefore difficult to justify exclusion of *O. latifrons* from the genus. *O. latifrons* is known only by incomplete cranial remains and until more complete specimens are available it is retained in *Osmeroides. Osmeroides latifrons* is most nearly related to *O. levis.* With this species it shares such features as smooth cranial bones, a very shallow otic region of the neurocranium with large otic bullae, a membranous interorbital septum and small dentary teeth which are decidedly pointed. With *O. lewesiensis* it shares but one character, a very broad parasphenoid.

The cranial anatomy of *O. latifrons* suggests a morphotype for the Albulidae and Pterothrissidae. Evolution of the latter fishes from *O. latifrons* would primarily involve loss of the medial ridge of the sub-epiotic fossa ; deepening of the trough upon the skull roof ; a general enlargement of the sensory canals with a reduction in their bony protection ; reduction or, in the case of the Albulidae, loss of ectopterygoid teeth ; expansion of the ectopterygoid process to contact the infraorbitals ; development of an inferior mouth ; development of an inflected dentary margin with consequent approximation of the jaw rami in the ventral mid-line and reduction or loss of the gular plate. In three features *O. latifrons* resembles the Albulidae rather than the Pterothrissidae ; the position of the quadrate/mandibular articulation, the broad parasphenoid and the irregular shape of the parietals. The first two of these similarities would not exclude *O. latifrons* from the ancestry of the Pterothrissidae since the position of the lower jaw articulation varies within each albuloid family and a broad parasphenoid is a basic albuloid character, also found in the primitive *Osmeroides lewesiensis*. The shape of the parietals, however, is a character of the Albulidae not found in the Pterothrissidae. This similarity is noted here, but no conclusions are drawn, as the phylogenetic implications of parietal shape are not understood.

Genus ***DINELOPS*** Woodward

1907 *Dinelops* Woodward : 121.

DIAGNOSIS. See Woodward (1907 : 121).

TYPE AND ONLY SPECIES. *Dinelops ornatus* Woodward.

Dinelops ornatus Woodward

1907 *Dinelops ornatus* Woodward : 121, pl. 24, figs. 4–6.

DIAGNOSIS. See Woodward (*op. cit.*).

HOLOTYPE. B.M.N.H. 39432, an incomplete cranium from the Upper Cenomanian of Kent.

MATERIAL. Only three specimens are known, the holotype and the paratypes B.M.N.H. 49091 and P.1812. The specimens consist of incomplete cranial remains and parts of the trunk from the Lower Chalk of S.E. England.

REMARKS. The affinities of this genus are problematical. Woodward (1907) stated that *Dinelops* resembled *Osmeroides*, a view which, with reservation, is upheld here.

The skull roof is relatively broad above the cranial vault but tapers sharply immediately anterior to the level of the autosphenotic spine, as in *Osmeroides latifrons*. The roofing bones are ornamented with coarse rugae which, unlike any species of *Osmeroides*, extend on to the dermethmoid. Above the cranial vault there is a median frontal depression but it is weakly defined. A medial branch of the supraorbital sensory canal opens on to the surface of the frontal above the hind end of the orbit and continues forward in a shallow trough, a condition similar to that of *Albula*.

The supraorbital, as in *Osmeroides*, is large and ornamented posteriorly.

The orbit is relatively large, larger than in any species of *Osmeroides*, and surrounded by a series of six canal-bearing infraorbitals. The sixth member, the dermosphenotic, is known by small fragments. The bones are thin, as in *Osmeroides latifrons*, and devoid of ornamentation. The posterior infraorbitals are wide, as in *Elops*, but the fourth is distinctively very shallow.

Of the upper jaw only the maxilla is known. It is totally unlike that of *Osmeroides*. The maxilla is straight and extends back to beneath the centre of the posterior infraorbitals. Anteriorly the maxilla is narrow and bears a prominent palatine cup before ending in a slightly expanded maxillary head. Woodward (1907) suspected the presence of only one supramaxilla, but the specimens are too imperfect to confirm this suspicion. The teeth are unknown but a series of moderately large alveoli set in a single row indicate a dentition unlike that of *Osmeroides*. The alveoli are only weakly delimited from one another and in some parts of the bone the teeth appear to have been set in a continuous groove.

The quadrate/mandibular articulation occurs well behind the eye, beneath the occiput. The mandible is deep throughout and a well-developed coronoid process is absent. B.M.N.H. 49091 is the only specimen showing the dentition. At the anterior end of the jaw the teeth are arranged in a band about four teeth wide. Behind this level there is a single row of prominent alveoli in which were set somewhat larger teeth. Lateral to this row of prominent teeth there are much smaller teeth, while towards the anterior end of this series small alveoli indicate that there may have been a medial row of very small teeth. The teeth are pointed. The absence of jaws in the type specimen makes positive identification of this jaw (B.M.N.H. 49091) difficult (Woodward 1907 only tentatively assigned this specimen to *Dinelops*). However, the ornamentation upon the mandible is very similar to that of the roofing bones.

The postcranial skeleton is even more poorly known. There are approximately 14 rays in the pectoral fin which was held low down on the body. The dorsal fin was situated above the pelvic fins and relatively far back.

The scales are large, almost circular and marked only by fine circuli. A few scales exhibit fine granulations in the posterior field.

The characters of the skull roof and supraorbital agree with those of the Osmeroididae. The jaws and dentition are, however, decidedly different and more advanced than *Osmeroides*. Failing knowledge of the neurocranium, *Dinelops* is tentatively retained in association with *Osmeroides*.

Family **PTEROTHRISSIDAE** Gill, 1893

DIAGNOSIS. Albuloid fishes in which the snout is elongated; mouth inferior. Ethmoid commissure incomplete, running through premaxillae. Supraorbital sensory canal not extending on to parietal. Occipital condyle formed entirely by basioccipital. Interorbital septum membranous. Lateral ethmoid not sutured to the parasphenoid, which is narrow. Parasphenoid and endopterygoid with conical teeth opposed by a similar dentition upon the basihyal and basibranchial tooth plates. Vomer edentulous. Premaxilla, maxilla and dentary with small, needle-like teeth. Posterior infraorbitals narrow, incompletely covering the cheek. Supraorbital small. Hyomandibular-metapterygoid foramen developed. Premaxilla tightly bound to the mesethmoid; maxilla moving independently; a single ovoid supramaxilla. Mandible with prominent coronoid process. Branchiostegals less than 10 in number. Gular plate absent. Dorsal fin elongated, anal fin short based. Caudal skeleton with two or three uroneurals. Inner caudal rays of each lobe without expanded bases. Principal caudal rays preceded by numerous basal fulcra, many of which are unsegmented and lie free in the body musculature. Caudal scutes absent.

Genus ***PTEROTHRISSUS*** Hilgendorf, 1877

1877 *Pterothrissus* Hilgendorf : 127.
1877 *Bathythrissa* Günther : 443.

Diagnosis. Pterothrissidae in which the interorbital distance is approximately one-quarter of the length of the neurocranium. Parasphenoid teeth extending to mid-orbital level. Maxilla with 6–7 teeth. Coronoid process forwardly directed and situated in the anterior third of the mandible. Branchiostegals six in number. Vertebral column with never less than 100 vertebrae.

Type-species. *Pterothrissus gissu* Hilgendorf.

Remarks. The genus is known by two species, the type-species, occurring off the coasts of Japan, and *P. belloci* Cadenat from off tropical West Africa. Both species are inhabitants of deeper waters. Poll (1953) records that most specimens of *P. belloci* have been found at the edge of the continental shelf. Information on *P. gissu* is imprecise but Okada (1960) states that it is found in ' moderately deep water '. Specimens of *P. belloci* were not examined but it is obvious from the description given by Poll (1953) that it closely resembles *P. gissu.* The main differences appear to be in the relatively greater length of the head and eye in *P. belloci,* and the lateral line scale count (85–90 in *P. belloci,* 99–112 in *P. gissu*).

Previous osteological information on *Pterothrissus* is scanty. Ridewood (1904) briefly noted some differences between *Pterothrissus gissu* (termed *Bathythrissa dorsalis* in that publication) and *Albula.* Gosline (1961) referred to the caudal structure and snout, and Monod (1968) described and figured the tail of *P. belloci.*

Pterothrissus gissu Hilgendorf

(Text-figs. 60–69)

1877 *Pterothrissus gissu* Hilgendorf : 127.
1877 *Bathythrissa dorsalis* Günther : 443.

Diagnosis. *Pterothrissus* reaching 400 mm S.L. Length of head equal to 25–26 per cent of the standard length. Maximum depth of the head at the occiput and equal to 50 per cent of the head length. Diameter of orbit 27–30 per cent of head length. Dorsal fin composed of 58–60 rays, anal 11–12 rays, pectoral 15 rays, pelvic 10 rays. 99–112 scales in lateral line. Transverse scale count at dorsal fin origin is 7 above and 8 below the lateral line.

Material. Four specimens were used in the preparation of the following osteological description. Three were donated by Prof. T. Abe of Tokyo University (221 mm, 236 mm and 220 mm S.L.). The fourth is a larger specimen, B.M.N.H. 1903.5.14.142.

DESCRIPTION. *Neurocranium.* The neurocranium is shown in dorsal, lateral, ventral and posterior views in Text-figs. 60, 61, 62 and 63. It is long and shallow with a slightly elongated snout which is turned downwards at its tip imparting to the head a characteristic albuloid appearance. Cartilage forms much of the ethmoid and nasal capsules and occupies large interspaces between certain bones in the otic region.

The ethmoid consists of a median vertical plate of cartilage which expands anteriorly to meet the contours of the dermethmoid above and the vomer below. Along the dorsal surface of the ethmoid there is a thin layer of perichondral bone. Dorsally this mesethmoid is overlain by a large dermethmoid, an element formed by a horizontal plate with a prominent vertical ridge on the dorsal surface. The ridge is pierced by a large fenestra, while anteriorly inclined struts link the vertical ridge with the horizontal portion. Beneath each strut there is an articular facet receiving the head of the premaxilla. The facet is formed by the perichondral mesethmoid.

The vomer is edentulous and narrow, unlike that element in albulids and osmeroidids. Anteriorly the head of the vomer is slightly expanded and is not clearly separable from the mesethmoid. The head of the vomer is produced ventrally as a stout median ridge which is semicircular in lateral view.

Each lateral ethmoid is represented by thin perichondral bone which covers the posterior and part of the lateral wall of the nasal capsule. Laterally the lateral ethmoid bears a stout ridge which receives ligaments from the posterior process of the palatine. A single foramen in the transverse wall of the lateral ethmoid transmits the olfactory tract, nasal artery and the superficial ophthalmic branches of V and VII. The lateral ethmoid is separated from its fellow by a narrow strip of ethmoid cartilage.

The frontal is narrow anteriorly where it is raised in the mid-line to form a ridge lying in continuity with the ridge on the dermethmoid. Above the orbit the lateral margin of the frontal forms a structure resembling a mudguard. Medial to this ' mudguard ' there is a shallow trough which ends posteriorly in a large sensory pore. The nasal lies above the anterior end of the frontal and the posterior region of the dermethmoid. Each nasal is formed by an anterior and larger posterior ossicle, each barely larger than the contained sensory canal. Both ossicles are open dorsally along their entire length. The presence of two ossicles composing the nasal element is noted elsewhere among elopiforms (*Elops*, *Megalops* and *Tarpon*) and is a reflection of a general elopiform tendency towards fragmentation of the snout elements.

The rectangular parietal is longer than broad and meets its partner over much of its length. A rebate developed along the posterior margin of the parietal contains the central portion of the supratemporal commissure. The parietal is perforated by several small pores (Text-fig. 60) and although the precise disposition of these pores varies from specimen to specimen there appears to be a longitudinal and a transverse series. Such an arrangement of pores is similar to those within the anterior and middle pit-lines of halecostomes, but in the latter fishes the pores are linked by shallow grooves, not seen in *Pterothrissus*.

The dermal portion of the pterotic forms the dorso-lateral corner of the skull roof. The otic sensory canal ran within a shallow groove along the lateral edge of the pterotic. A narrow rebate along the posterior margin of the pterotic, which lies

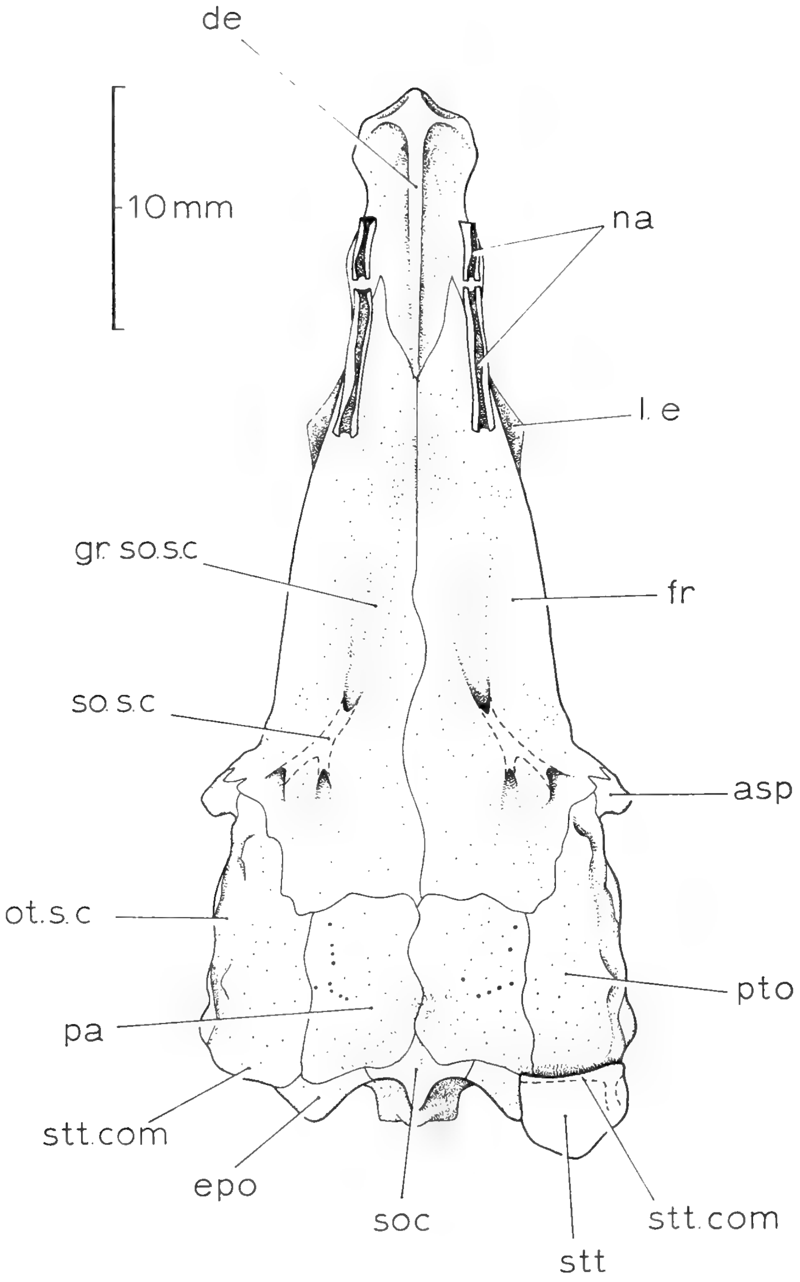

Fig. 60. *Pterothrissus gissu* Hilgendorf. Neurocranium in dorsal view. This and Text-figs. 61–69 are composites from several specimens.

adjacent to an open groove upon the supratemporal, contains the lateral portion of the supratemporal commissure. In lateral view (Text-fig. 61) the endochondral portion of the pterotic is seen to form the greater part of the dilatator fossa, the posterior half of the hyomandibular facet and the roof of the deep subtemporal fossa. Beneath the hyomandibular facet the pterotic is marked by an arc-shaped swelling which marks the path of the horizontal semicircular canal. The medial surface of the pterotic forms the roof, the lateral wall and part of the floor of the post-temporal fossa.

In dorsal view the supraoccipital (Text-fig. 60) is seen to separate the parietals posteriorly. Two antero-laterally directed wings of the supraoccipital extend beneath the parietals and contact the autosphenotic. The anterior wings also form the inner wall of the post-temporal fossae. In posterior view (Text-fig. 63) the supraoccipital is small, semicircular and separated from the exoccipital by a large area of cartilage. The supraoccipital crest is very small.

Between the supraoccipital and pterotic lies the irregularly shaped epiotic (Text-figs. 60, 63). A narrow band of cartilage separates the epiotic from the exoccipital. The posterior vertical semicircular canal runs through the epiotic and its path may be seen externally as a ridge running along the medial margin of the post-temporal fossa and forming an arc above the subepiotic fossa. The epiotic process is weakly developed.

The exoccipital (Text-fig. 61) forms the posterior wall of the subtemporal fossa and part of the large otic bulla. Three foramina are present on the lateral face of the exoccipital : anteriorly there is a glossopharyngeal foramen which is preceded by a shallow groove, then follows a small foramen for a blood vessel, and posteriorly a large, ventrally directed vagus foramen. The posterior face of the exoccipital (Text-fig. 63) forms the ventral half of the subepiotic fossa. The exoccipital meets its fellow above and below the foramen magnum. The lateral and posterior faces of the exoccipital meet in a pronounced thickening, within which run the horizontal and posterior vertical semicircular canals.

At the lower margin of the opening to the post-temporal fossa there is an area of cartilage between the exoccipital, pterotic and epiotic. Covering this cartilage is the intercalar which, as in all albuloids, is relatively small. The posterior surface of the intercalar is ridged, providing a surface of attachment for a tendon from the intercalar limb of the post-temporal. Laterally the intercalar curves antero-ventrally and in one specimen examined (Text-fig. 61) forms the dorsal margin of the vagus foramen.

The basioccipital forms the occipital condyle, the posterior portion of the myodome roof and the walls of the saccular recess of either side. The vertebral-like expansion of the basioccipital shows a deep notochordal pit, which is not quite symmetrical since the ventral margin lies more horizontally than the dorsal. Between the bullate portion and the occipital expansion the lateral surface of the basioccipital is rough, providing an anchorage point for a strong ligament passing to the cleithrum/supracleithrum overlap. Ventrally the basioccipital is marked by a shallow groove which is continuous with a small groove upon the parasphenoid.

The prootic is, as usual, a bone of complex shape. The lateral face contributes to the formation of the hyomandibular facet, the subtemporal fossa and the otic

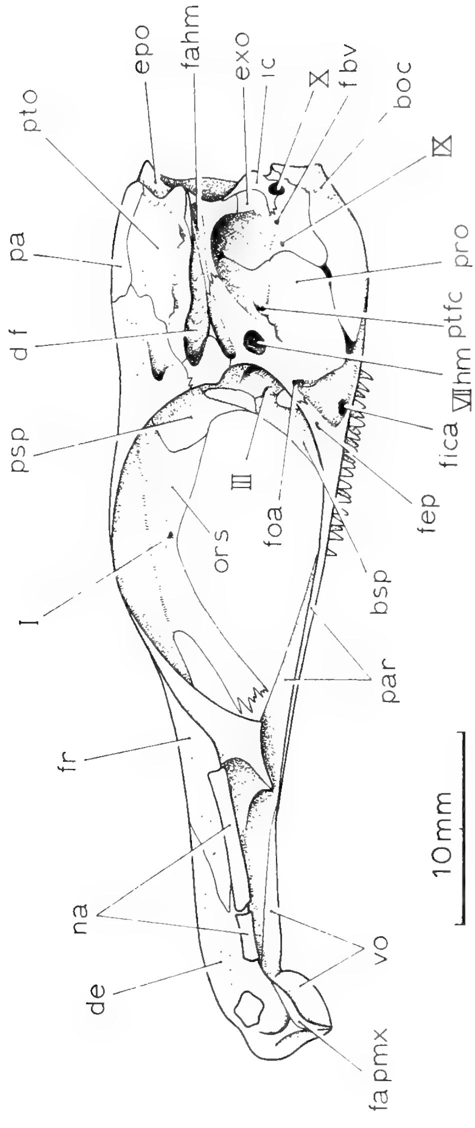

Fig. 61. *Pterothrissus gissu* Hilgendorf. Neurocranium in left lateral view.

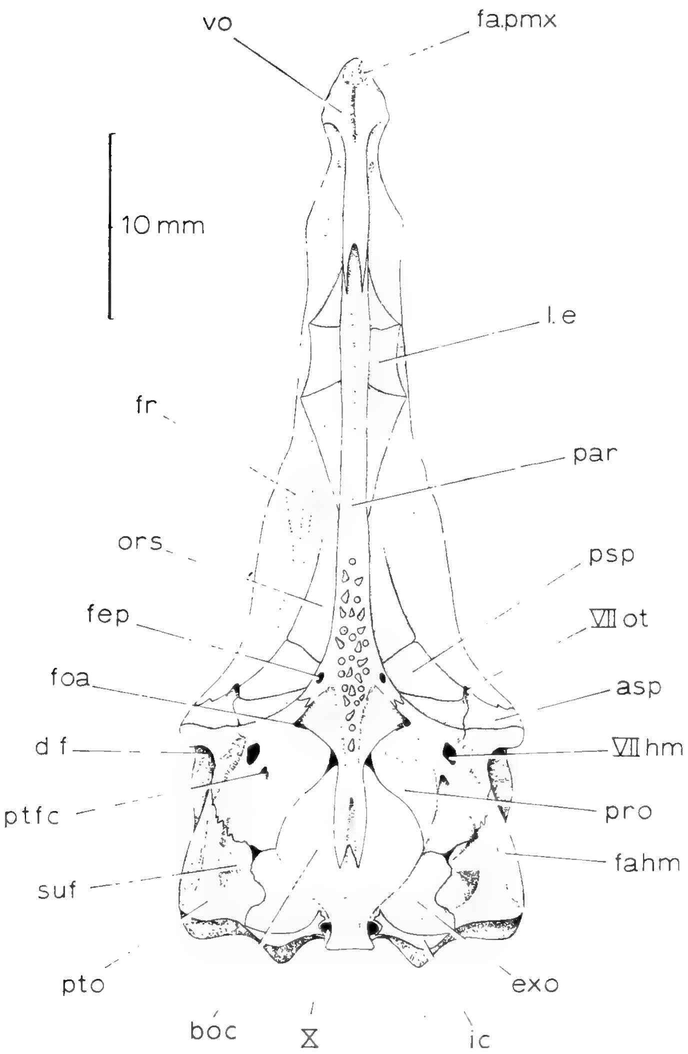

FIG. 62. *Pterothrissus gissu* Hilgendorf. Neurocranium in ventral view.

bulla. At two points the prootic fails to meet the basioccipital: anteriorly where these bones meet the parasphenoid and posteriorly where they meet the exoccipital. There are thus left two triangular interspaces, which even in the largest specimen examined remain open.

A large foramen for the hyomandibular trunk of VII opens directly from the pars jugularis, so that when the neurocranium is viewed laterally (Text-fig. 61) the trigeminal and facial foramina may be seen opening from the pars ganglionaris. The orbital artery enters the prootic at the base of a deep groove situated immediately above the ascending wing of the parasphenoid. The orbital face of the prootic is of

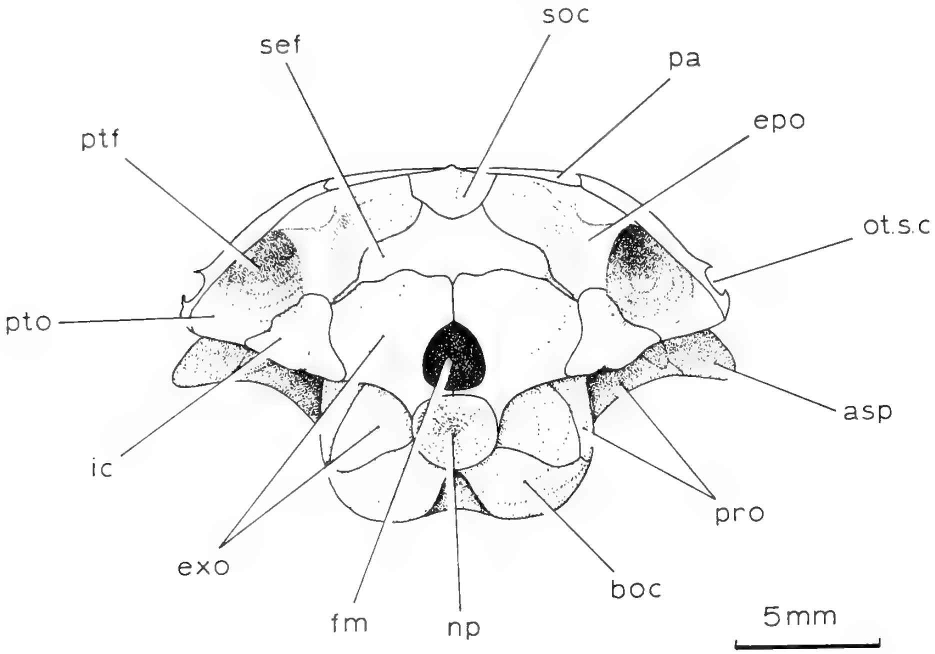

FIG. 63. *Pterothrissus gissu* Hilgendorf. Neurocranium in posterior view.

limited extent ; it is pierced laterally by the large anterior opening of the pars jugularis and medially by the oculomotor foramen. The relationships of the rami of V and VII to the pars ganglionaris and pars jugularis are similar to those described for *Osmeroides lewesiensis* (p. 99). The prootic bridge is narrow and separated from the basioccipital by cartilage. The anterior margin of the bridge is indented where it forms the posterior half of the hypophysial foramen. Posteriorly the abducens nerve pierces the prootic bridge.

The autosphenotic contacts the pterosphenoid medially and the prootic ventrally. Laterally the autosphenotic is produced as a short ' spine '. Postero-laterally the autosphenotic contributes to the dilatator fossa and the extreme anterior end of the hyomandibular facet. Much of the autosphenotic is overlain by the frontal. The otic branch of VII, which in most teleosts pierces the centre of the orbital face of the autosphenotic, here pierces the suture between the autosphenotic and pterosphenoid.

The pterosphenoid lies posterior to the orbitosphenoid, antero-medial to the autosphenotic and medial to the prootic. Part of the border of the optic foramen is formed by the pterosphenoid. The orbitosphenoid is quite large and in the largest specimen examined (B.M.N.H. 1903.5.14.142) is produced anteriorly as a single median plate which bifurcates distally and is connected to the lateral ethmoids by short ligaments. The surface of the orbitosphenoid is marked by a prominent groove anterior to the level where the olfactory tracts leave the cranial cavity.

The basisphenoid is ' Y '-shaped, each wing contacting the pterosphenoid and prootic in such a way as to exclude the latter from the optic foramen. The stem of the basisphenoid is expanded distally.

Throughout most of its length the parasphenoid is narrow, expanding only at the level of the short ascending wings. Both anteriorly and posteriorly the parasphenoid is marked by a median groove. Towards the rear of the orbit the parasphenoid bears approximately 30 teeth. Each tooth is conical with a rounded tip. The efferent pseudobranchial and internal carotid arteries pierce the parasphenoid at the level of the ascending wings.

Hyopalatine bones. The hyopalatine series of *Pterothrissus* is of a pattern characteristic of other pterothrissids and albulids but rather different from that in the primitive species of *Osmeroides* (*O. lewesiensis* and *O. levis*), which resemble the Elopoidei in this respect.

The hyopalatine series of *Pterothrissus* is long and shallow. The hyomandibular has a single broad articulatory head. The bone is thin in this region and this is reflected in the narrow hyomandibular facet on the neurocranium. A stout ridge runs the length of the hyomandibular shaft. Dorsally the posterior divisions of the levator arcus palatini muscle insert on this ridge, while ventrally the ridge serves as a site of origin for the A_2 division of the adductor mandibulae. Beneath the hyomandibular head the posterior margin is expanded to form a rounded opercular process. Upon the medial face a ridge is seen to grade into the opercular process ; to this ridge are attached the deeper fibres of the levator opercularis. The hyomandibular trunk of VII enters the hyomandibular on the medial surface near to the anterior end of the head. Within the bone the nerve splits to two subequal branches, both of which emerge on the posterior edge of the shaft. The upper, smaller, opercular branch leaves the bone immediately beneath the opercular process while the

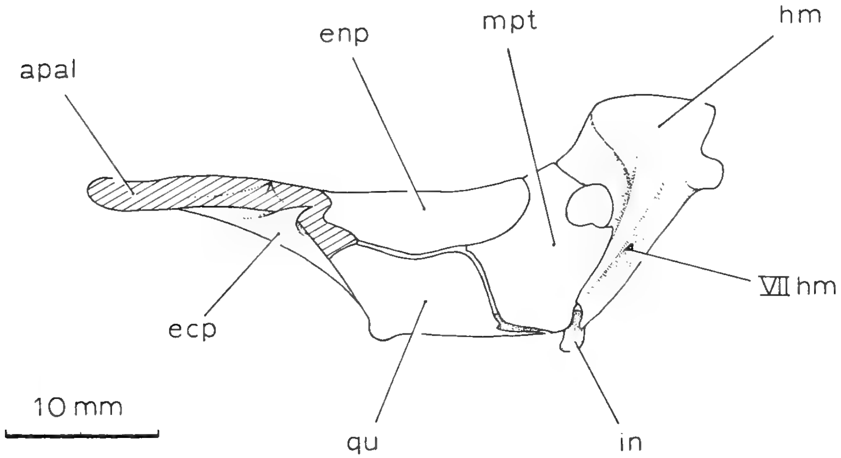

FIG. 64. *Pterothrissus gissu* Hilgendorf. Hyopalatine bones of left side in lateral view. Cartilage hatched.

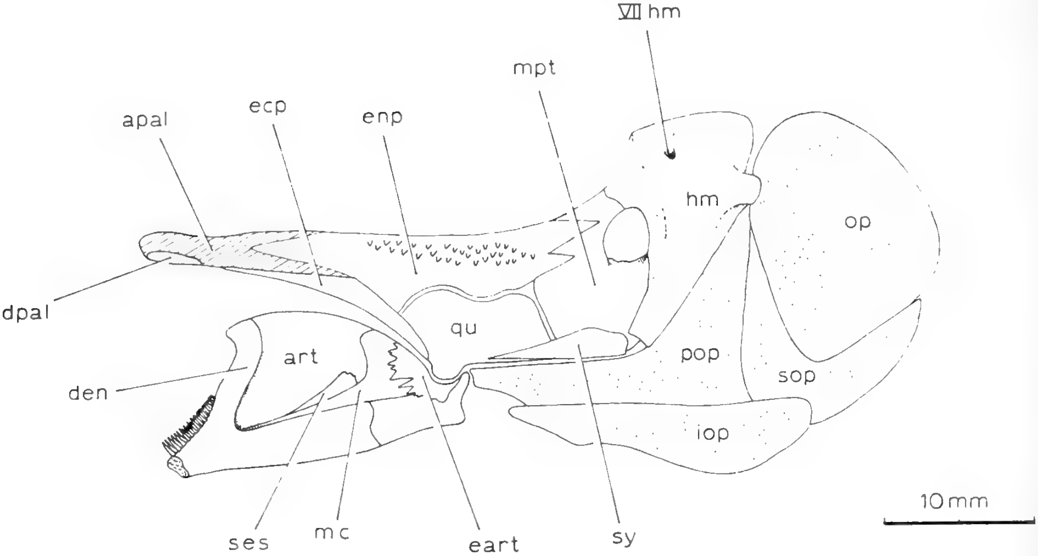

FIG. 65. *Pterothrissus gissu* Hilgendorf. Hyopalatine bones, opercular series (stippled) and mandible of right side in medial view. Cartilage hatched.

lower, mandibular branch opens laterally into a shallow groove mid-way along the length of the shaft. A thin anterior wing is developed in the dorsal half of the hyomandibular. There is no overlap of the hyomandibular by the metapterygoid. Instead, there is a large foramen between these bones, the hyomandibular-metapterygoid foramen, through which passes a deep division of the levator arcus palatini to insert upon the medial face of the metapterygoid.

The quadrate is basically fan-shaped with the postero-ventral angle produced as a short spine. The ' posterior ' quadrate margin lies horizontally as in most albuloids.

The endopterygoid is somewhat longer than broad. A patch of approximately 40 teeth, similar in shape to those on the parasphenoid, is borne by the convex palatal surface. The ectopterygoid of *Pterothrissus*, unlike that of *Osmeroides*, is narrow and only meets the endopterygoid over a short distance (Text-fig. 64). The ectopterygoid bears a few tiny teeth which are difficult to see in ' unprepared ' specimens. Dorsally the ectopterygoid process is relatively small and is directed towards the infraorbital bones. A short ligament connects the process with the infraorbital series at the junction of the first and second infraorbitals.

There is no ossified autopalatine. The palatine cartilage articulates with the mesethmoid by a simple rounded head, the anterior process of the palatine. Beneath the lateral ethmoid there is another dorsally directed process, the posterior process of the palatine. The dermopalatine is represented by a small, toothless, oval ossification attached to the ventral surface of the palatine cartilage.

Dermal upper jaw. The premaxilla is stout with an inwardly turned head bearing a single articulatory facet. A tough ligament runs from the external face of the premaxilla head to the dorsal margin of the dermethmoid ridge. This ligament, the tight fit of the articulatory facet and the presence of tough connective tissue combine to make the premaxilla practically immovable. The lateral surface of the premaxilla is perforated by three or four pores which lead to a sensory canal running through the bone. Posteriorly the alveolar process of the premaxilla is tapered and received in a small notch in the maxilla.

The maxilla is narrow and stout anteriorly where it curves inwards to articulate with the ethmoid via a biconcave cartilaginous pad. Posteriorly the maxilla is thin and ovoid in lateral view, save for a small excavation into which a single oval supramaxilla fits.

The majority of the upper jaw teeth are found on the premaxilla. The oval margin of the premaxilla is clothed with many small needle-like teeth which point towards the buccal cavity. The maxilla has a feeble dentition, there being only five or six pointed teeth set in a single row.

Mandible. The mandible is short and deep with a prominent coronoid process situated anteriorly. Ventrally the margins of the dentary and articular are inflected and form a broad shelf. From the lateral face of this shelf a thin flange of bone projects and this forms a partial protection for the mandibular sensory canal.

The dentary is narrow anteriorly and is markedly turned inwards at the symphysis. In shape, size and disposition the numerous dentary teeth resemble those on the premaxilla.

The articular is slightly larger than the dentary. Posteriorly it forms the outer aspect of the articular facet. The endochondral articular (endosteal articular of Ridewood 1904) is distinguishable by the spongy installation nature of the bone but it appears

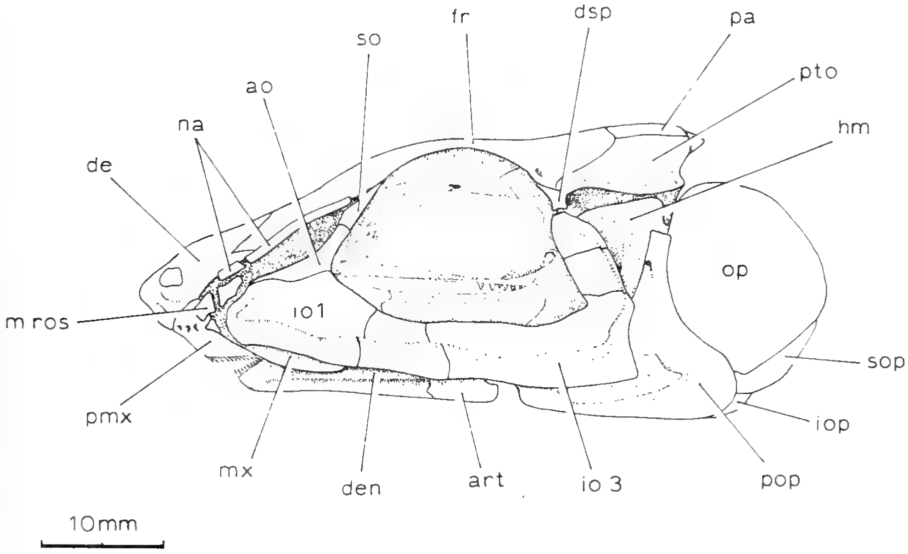

FIG. 66. *Pterothrissus gissu* Hilgendorf. Cranium in left lateral view.

to be fused with the articular. The Meckelian cartilage rests on a ledge on the medial face of the mandible. The sesamoid articular is partially embedded within the cartilage.

Circumorbital series. The circumorbital series is composed of six infraorbitals, three rostral ossicles, an antorbital and a supraorbital.

The orbital margin of the six infraorbitals is rolled laterally so forming a ventrally incomplete tube round the sensory canal. The first infraorbital is large with a rounded anterior margin. Much of the maxilla is covered by this element. Posteriorly the first infraorbital partially overlies the second of the series but the connection between these bones is flimsy and they separate easily. As is usual in elopiforms the third infraorbital is the largest of the series. This element is angled and the posterior margin exhibits a shallow indentation. The fourth and fifth infraorbitals form a narrow inclined strut. The sixth infraorbital, or dermosphenotic, has no direct contact with any other bone but lies free in the skin. In all, the posterior infraorbitals are quite distinct from those of *Albula,* as may be seen by comparing Text-figs. 66 and 80.

The antorbital is a narrow, elongate ossification which together with a similarly shaped supraorbital forms a flexible strut serving to help expand and contract the supraorbital nasal diverticulum. The importance of this strut in relation to the functioning of the diverticulum has been noted by Derschied (1924) and Gosline (1961). The three small rostral ossicles lie free from one another and from any neighbouring bone. The margins of each ossicle are rolled over to contain the sensory canal.

Opercular series. The shape of the operculum, suboperculum, preoperculum and interoperculum may be seen in Text-figs. 65 and 66. The suboperculum is notable in having a particularly long dorsally directed anterior wing which almost reaches to the level of the opercular process of the hyomandibular. The interoperculum, which resembles a branchiostegal ray, is joined anteriorly to the rear of the mandible and posteriorly to the suboperculum by ligaments. The preopercular sensory canal runs within a short bony tube dorsally and is protected ventrally by a large flange of bone. The middle portion of this canal lies free in the skin.

Cephalic sensory canal system. The sensory canals of the head are more open than in any other albuloid. For the most part the canals lie within troughs covered by taut skin.

The supraorbital canal passes through the frontal for a very short distance, much of its length being accommodated within the frontal trough. Anteriorly the supraorbital canal continues within the gutter-like nasal and ends blindly at the tip of the dermethmoid. The supraorbital canal connects with its partner of the opposite side through a large fenestra in the dermethmoid ridge. In two of three specimens examined in this respect a single neuromast was observed in the skin at the base of this fenestra (a feature previously noted by Gosline 1961) and this neuromast, like others of the supraorbital canal, is supplied by the superficial ophthalmic nerve. In the third specimen examined no neuromast could be seen.

The otic sensory canal lies within a groove upon the pterotic. Anteriorly the otic canal joins the supraorbital and infraorbital canals in the skin immediately above the dermosphenotic. Posteriorly the otic canal joins the preopercular canal and the supratemporal commissure at the postero-lateral angle of the pterotic. The lateral line passes back through the supratemporal to open on the undersurface of that bone.

The infraorbital canal runs within the large infraorbital trough. Anteriorly the canal splits into two branches : dorsally there is a short antorbital branch which runs over the antorbital and ends blindly at the dorsal end of that element ; anteriorly an ' ethmoid ' branch runs through the rostral ossicles before passing through the premaxilla to end blindly within that bone. The triradiate union of the ' ethmoid ' branch, antorbital branch and the main infraorbital canal lies in the skin just anterior to the first infraorbital. At one point, above the gap between the middle and posterior rostral ossicles, the ' ethmoid ' canal and supraorbital canals are only separated by membrane.

The course of the preopercular sensory canal has been described above. Ventrally this canal continues within the deep trough upon the dentary and articular as the mandibular sensory canal.

Hyoid arch and gill arches. The ceratohyal is separated by a band of cartilage into a semicircular posterior element and a longer, waisted anterior ceratohyal. Two hypohyals are represented by perichondral ossifications around a single large cartilage. The smaller dorsal hypohyal articulates with the posterior face of the basihyal and the ventral hypohyal receives a ligament from the urohyal. The afferent hyoidean artery pierces the medial surface of the ventral hypohyal and passes into a groove on the lateral surface of the anterior and part of the posterior ceratohyal. Six branchiostegal rays are attached to the medial surface of the ceratohyal elements. The uppermost (posterior) ray is the only member of the series associated with the posterior ceratohyal.

The basibranchium is formed by a partially ossified basihyal and three separately ossified basibranchials. The fourth basibranchial is entirely cartilaginous. The basihyal tooth plate is large and bears approximately 15 pointed teeth posteriorly. A large tooth plate overlies the first three basibranchials and like the fourth basibranchial tooth plate bears teeth similar to those upon the basihyal tooth plate. The teeth associated with the basibranchium become smaller posteriorly.

The first two hypobranchials articulate with the posterior surface of their respective basibranchials. The reduced third hypobranchial articulates with the centre of its basibranchial. Of the five ceratobranchials the first three articulate with the distal ends of the hypobranchials while the fourth and fifth are connected to the fourth basibranchial by ligaments.

The dorsal arch elements are represented by epibranchials, infra- and suprapharyngobranchials. There are four epibranchials associated with the first four ceratobranchials. The first epibranchial is simple, showing a double articulatory head. The anteriorly directed head receives the posterior end of the small rectangular first infrapharyngobranchial. The posterior head of the epibranchial is directed dorso-medially and articulates with a cartilaginous first suprapharyngobranchial. The second epibranchial, like the third, shows a marked bifid head with the anteriorly directed limb being larger than the dorso-medially directed process. The anterior head articulates with the posterior margin, or in the case of the third epibranchial with the lateral margin, of their respective infrapharyngobranchials. The anterior ends of the second and third infrapharyngobranchials have two heads, one directed antero-medially, the other directed antero-laterally and joined by cartilage to the epibranchial of the preceding arch.

The fourth epibranchial is unusual in showing three dorsal processes. Basically this element has two heads, like the anterior epibranchials, but the posterior projection has become subdivided. The significance of this subdivision is not clear. The fourth infrapharyngobranchial has the same relationship to its epibranchial support as those anteriorly, but is represented by a simple semi-ovoid cartilage having no connection with the antecedent epibranchial.

Upper pharyngeal tooth plates are associated with the second, third and fourth infrapharyngobranchials. The third infrapharyngobranchial tooth plate is triangular while the fourth is divided into two sections, one associated more closely with the epibranchial, the other more closely associated with the infrapharyngobranchial.

In addition to the basibranchial and upper pharyngeal dentition there are tooth plates associated with the oral surface of all cerato- and epibranchials and the first two hypobranchials. The tooth plates associated with these elements appear to be aligned in three rows, anterior, middle and posterior. The plates of the anterior row of the first arch are modified into gill-rakers which consist of a bulbous, toothed head supported on a slender stalk. The tooth plates of the posterior row on the fifth ceratobranchial are enlarged to form the lower pharyngeal tooth plate. Each tooth plate bears several pointed teeth.

Pectoral girdle and fin. The main body of the post-temporal is represented by a flat plate of bone, pierced laterally by the lateral line. Two processes arise from the ventral surface of the main body : projecting anteriorly there is a spinous epiotic or dorsal limb, while ventrally there is a thicker intercalar or ventral limb.

The supracleithrum is elongate, rounded at both ends, and shows a slight indentation in the posterior margin. The lateral line passes obliquely through the upper half of the bone. The cleithrum is large. Above the fin insertion the bone is expanded to provide support for the large axillary scale. Anteriorly the cleithrum is tapered and is joined to its partner by a strip of tough connective tissue. Throughout its length the anterior margin of the cleithrum is turned medially providing a broad area of insertion for the sternohyoideus musculature.

The coracoid is aliform and, unlike that of elopoids, does not extend to the tip of the cleithrum. Between the anterior and posterior connections of the cleithrum and coracoid there is a slit-like fenestra. The scapula is circular save for a deep notch anteriorly which represents an incomplete scapular foramen. The mesocoracoid is stout, particularly ventrally where it contacts the scapula and coracoid through a large area of cartilage. As in most albuloids the anterior margin of the mesocoracoid arch has contact with the cleithrum over much of its length.

All but the outermost pectoral fin-ray are supported by the four proximal radials, which although of basic teleostean form, articulate with cartilage and are not, as is usual, directly related to the scapula and coracoid. The outermost fin-ray articulates both directly and indirectly with the scapula. Between the halves of the outermost ray there is a small ovoid element consisting of an ossified core surrounded

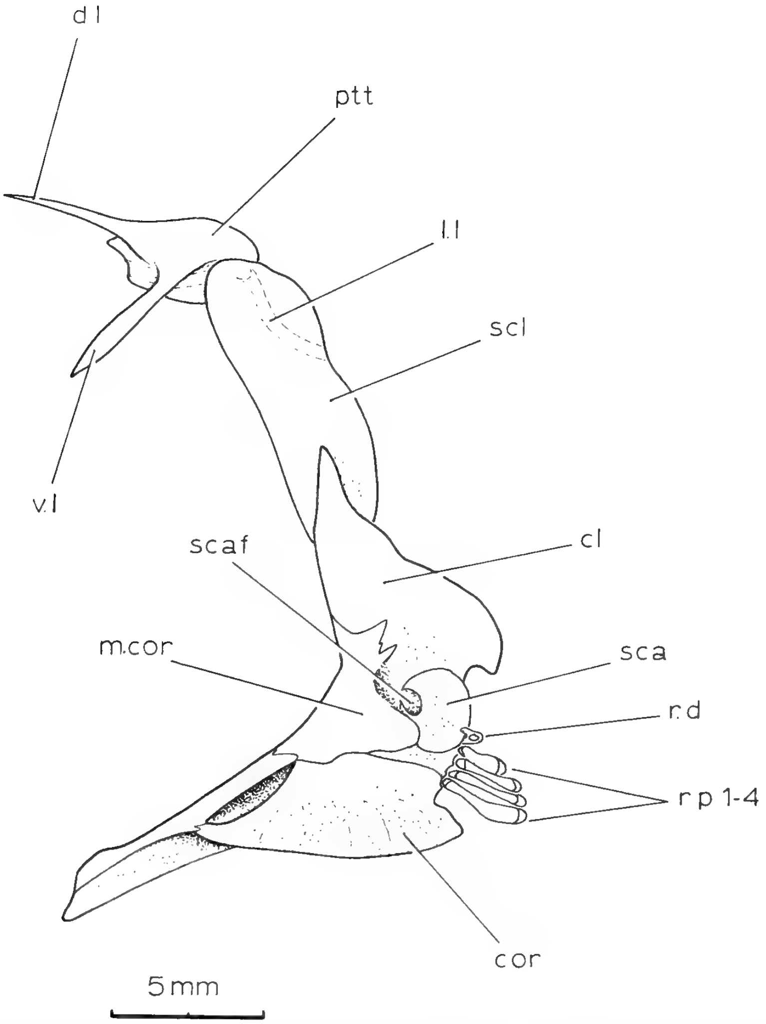

FIG. 67. *Pterothrissus gissu* Hilgendorf. Pectoral girdle of right side in medial view.

entirely by cartilage. In shape and disposition this radial resembles members of the cartilaginous distal radial series. This partially ossified distal radial, together with the base of the outermost fin-ray, fits into the depression upon the scapula.

Of the 16 pectoral fin-rays only the first is unbranched. Little may be said of the length of the rays since the tips of the fin-rays were missing in all specimens examined. To judge by the width, the second is the longest pectoral ray. A small pectoral splint bone is associated with the base of the outermost ray. The proximal end of the splint is turned slightly upwards and markedly inwards to contact the small distal radial mentioned above. It is therefore unlike the pelvic splint bone in which the proximal end lies free in the body musculature.

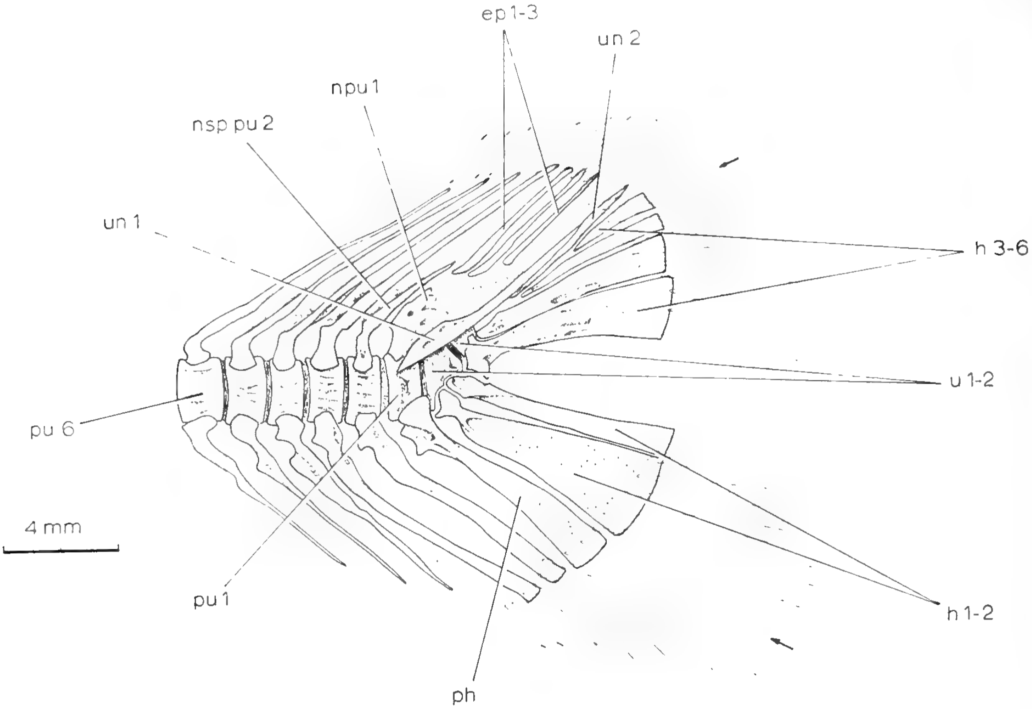

FIG. 68. *Pterothrissus gissu* Hilgendorf. Caudal skeleton in left lateral view. Arrows indicate upper and lower principal caudal fin-rays.

Pelvic girdle and fin. The pelvic fin originates mid-way between the snout and the caudal peduncle. The fin is supported by a triangular pelvic bone. A narrow band of cartilage forms a cap along the posterior margin of the pelvic bone. Only the innermost pelvic radial is ossified. There are 10 pelvic fin-rays, the outermost unbranched and the third apparently the longest. A large pelvic splint is associated with the base of the upper half of the outermost (the first) fin-ray.

Vertebral column. Of the 107 vertebrae 35 are caudal. Each centrum is amphicoelous and pierced for the passage of the constricted notochord. Most centra throughout the column are marginally deeper than long but the first sixteen and the posterior three or four are almost twice as deep as long. The lateral surface of each centrum is marked by several longitudinal ridges.

The neural arches are autogenous. Those upon the anterior 45 centra are expanded distally and bear narrow neural spines. Throughout the abdominal region the spines are represented by separate lateral halves. Short, stout, autogenous parapophyses are found throughout the abdominal region. Those posteriorly are somewhat longer than those anteriorly. The first complete haemal arch and spine occurs on the seventy-sixth centrum.

The pleural ribs are short and slender and partially encircle the abdominal cavity. Epineural intermuscular bones are associated with the first 67 neural arches. Those associated with the first 49 are attached to the base of the neural arch, but thereafter they are inserted nearer to the distal end of the arch. Short epipleural intermusculars are associated with the first 73 parapophyses. Anteriorly there are 11 sigmoid supraneurals. The anterior members of the series are larger than those posteriorly.

Median fins. The dorsal fin is elongate, equal in length to half the standard length and composed of 58–60 fin-rays. The first four fin-rays are unsegmented and unbranched. The fifth is segmented and the sixth and those succeeding it are branched at least twice. The fin-rays are supported by 56–58 pterygiophores. Most of the pterygiophores are composed of separately ossified proximal, middle and distal radials but the first two, which between them support four fin-rays, are formed by a large compound radial and a separately ossified distal radial.

The anal fin originates beneath the seventy-fifth vertebra and is composed of 12 fin-rays of which the first three are unbranched and unsegmented, the next two are segmented but unbranched while the rest are both segmented and branched.

The caudal fin is deeply forked and the margin of each lobe is rounded. Eight centra, two ural and six preural, are involved in the support of caudal fin-rays. The ural centra are as long as deep, sharply upturned and show little or no ornamentation. The neural spines of the third to sixth and the haemal spines of the first to sixth preural centra are longer and stouter than their anterior counterparts. These structures also show the development of median wings basally. The neural spine of the second preural centrum varies; Gosline (1961) records a complete neural spine but in the four specimens I examined there is only a half spine, as in the specimen of *P. belloci* illustrated by Monod (1968). The neural arch of the first preural centrum is represented by a thin ossified structure above which there is a broad plate of cartilage which lies between the halves of the first uroneural posteriorly.

There are two narrow uroneurals. The first is long and the expanded proximal end partially covers the first preural centrum. The second uroneural is shorter, fails to overlap any centrum and extends beyond the distal tip of the first. Such a uroneural disposition is typical for more advanced albuloids.

There are six hypurals. The first and second hypurals articulate with the first ural centrum, the third and fourth are associated with the second ural centrum, and the fifth and sixth lie free. The base of the third hypural is expanded and partially encircles the centrum. The large gap between the second and third hypurals is a typical feature of the pterothrissid caudal skeleton. The epurals are represented by three splint-like elements forming a graded series.

As usual in ' lower ' teleosts there are 19 principal caudal fin-rays. The bases of the innermost principal rays are not expanded and do not overlap the hypurals to any significant degree (cf. elopoids). There are 14–16 basal fulcra dorsally and 7–8 ventrally. The anterior members of both series lie free in the musculature.

Squamation. The body is covered with cycloid scales. There are approximately 100 in the lateral line series while the transverse count at the origin of the dorsal fin is 7 above and 8 below the lateral line. Precise counts are difficult because of the condition of the specimens examined. Large axillary scales are associated with the pectoral and pelvic fins.

Each scale is generally rounded but has a straight anterior margin. The posterior margin is thin and frequently split. Lateral line scales, apart from a slight anterior

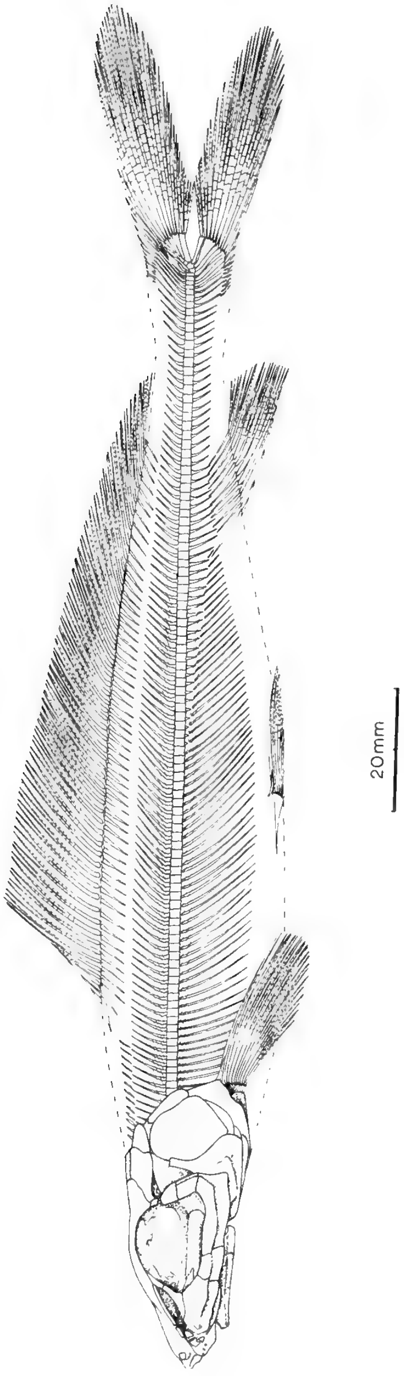

Fig. 69. *Pterothrissus gissu* Hilgendorf. Entire skeleton, scales omitted.

prominence, differ little from the other body scales. The position of the nucleus of the scale varies slightly according to the position of the scale on the body. Anterior scales show an anteriorly situated nucleus. The converse is true of those scales situated posteriorly. Five to eight short radii are found within the anterior field of the scale but they do not reach the nucleus. Between the radii the anterior edge of the scale is slightly scalloped. Radii are less numerous on lateral line scales and the margins are generally smoother. The dorsal, ventral and anterior fields show well-marked circuli. In the anterior field the circuli tend to break up to form numerous backwardly pointing tubercles. All scales have enclosed bone cells which are generally more numerous towards the edges of the anterior, dorsal and ventral fields.

Genus ***ISTIEUS*** Agassiz, 1844

1844 *Istieus* Agassiz : **5**, pt. 2, p. 91.

DIAGNOSIS. Pterothrissid fish in which the interorbital distance is equal to one-third of the length of the neurocranium. Parasphenoid tooth patch extending from beneath the lateral ethmoid to the level of the parasphenoid ascending wings. Maxilla bearing many teeth. Mandible with a weakly developed coronoid process situated in the posterior third of the jaw. Dentary teeth larger than those of the upper jaw.

TYPE-SPECIES. *Istieus grandis* Agassiz.

Istieus grandis Agassiz

(Text-figs. 70–73)

1833–44 *Istieus grandis* Agassiz : **5**, pt 1, p. 13 ; pt 2, p. 92, pl. 18.
1833–44 *Istieus microcephalus* Agassiz : **5**, pt 1, p. 13 ; pt 2, p. 94, pl. 17.
1833–44 *Istieus macrocephalus* Agassiz : **5**, pt 1, p. 13 ; pt 2, p. 94, pl. 16 (lower figure) (*errore*).
1858 *Istieus grandis* Agassiz ; Marck : 246.
1858 *Istieus microcephalus* Agassiz ; Marck : 246.
1863 *Istieus macrocoelius* Marck : 37, pl. 4, figs. 1–5.
1863 *Istieus mesospondylus* Marck : 38, pl. 5, fig. 1.
1873 *Istieus macrocoelius* Marck ; Marck : 59, pl. 2, fig. 2.
1885 *Istieus macrocoelius* Marck ; Marck : 253.
1901 *Istieus grandis* Agassiz ; Woodward : 67.
1954 *Istieus grandis* Agassiz ; Siegfried : 11, pl. 2, figs. 5, 6.

DIAGNOSIS. *Istieus* reaching 550 mm S.L. Length of head 30 per cent S.L., maximum depth of body approximately 22 per cent S.L. Operculum one-and-a-half times as deep as wide. 8–10 branchiostegal rays. Vertebrae 87–92, dorsal fin-rays 53–57.

HOLOTYPE. Imperfect fish, Muséum National d'Histoire Naturelle, Paris, from the Campanian of Sendenhorst, Westphalia, Germany.

Material. Seventeen specimens in the B.M.N.H. from the Campanian of Sendenhorst, Westphalia, Germany. The fish are mainly preserved in impression in a fine-grained, grey limestone. The bone, where present, is soft and poorly preserved. In studying the material rubber casts were used.

Remarks. In a great many features there is close agreement between the anatomy of *Pterothrissus* and *Istieus*. This similarity necessitates only a brief comparative description of *Istieus grandis*.

Description. *Neurocranium*. The neurocranium, like that of *Pterothrissus*, is long and shallow. The snout is less elongated than that of *Pterothrissus* and does not exhibit the sharp anterior curvature. In dorsal view (Text-fig. 70) several minor differences from *Pterothrissus* (Text-fig. 60) are evident ; the dermethmoid and pterotic of *Istieus* are relatively smaller, the parietal is only marginally longer than broad, and the frontal is wider, particularly above the orbit. As in *Pterothrissus*, the dermethmoid bears a prominent median ridge supported anteriorly by inclined struts, the lateral margin of the frontal is raised into a ' mudguard ' above the eye and the posterior margin of the pterotic shows a narrow rebate for the supratemporal commissure. In *Istieus* the nasal is represented by a long gutter-like element, there being no evidence of two separate ossicles as in *Pterothrissus*.

A lack of detail in the snouts of all the specimens leads one to suppose that, as in *Pterothrissus*, much of the ethmoid was cartilaginous. The lateral ethmoid of *Istieus* is the same shape as that of *Pterothrissus* but relatively larger.

Little is known about the lateral wall of the otic region. B.M.N.H. P.3885a shows an internal view of the right side, although little bone remains. This specimen shows that the bulla which contained the sacculith is large, the subtemporal fossa is deep and there is a deep depression posterior to the ascending wing of the paraspenoid. In all that may be seen the lateral wall of the braincase is similar to that of *Pterothrissus*.

The parasphenoid, as in *Pterothrissus*, is straight and narrow and runs from beneath the lateral ethmoid to beneath the middle of the otic region. Woodward (1901) stated that no parasphenoid teeth could be seen, but B.M.N.H. P.3885a clearly shows their presence. There are many more teeth on the parasphenoid than in *Pterothrissus*. Each tooth is conical with a rounded tip. The vomer is narrow and edentulous but does not show the semicircular median ridge seen in *Pterothrissus*.

Hyopalatine bones. The hyopalatine series, as in all pterothrissids, is longer than deep and the quadrate/mandibular articulation lies beneath the posterior half of the orbit.

The shape of the hyomandibular is very similar to that of *Pterothrissus* but the head is formed of thicker bone. Antero-ventrally the hyomandibular is partially overlapped by the metapterygoid, a feature not seen in *Pterothrissus*. However, the hyomandibular-metapterygoid foramen is developed in typical fashion. As in *Pterothrissus* the inner surface of the metapterygoid is grooved for the reception of the flattened symplectic.

The endopterygoid is relatively large and bears more teeth than in *Pterothrissus*. The teeth all appear to be conical but they probably varied considerably in size as witnessed by the irregular size of the alveoli in B.M.N.H. 35012. The topographical

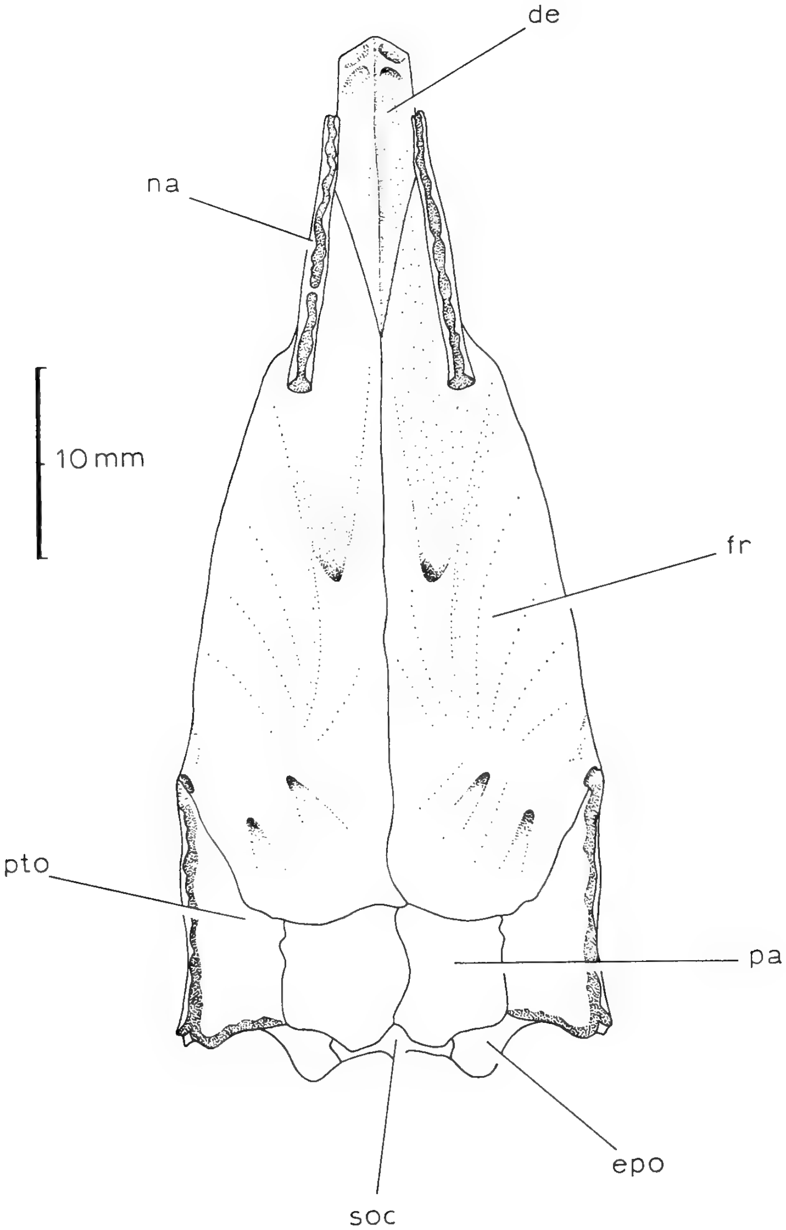

FIG. 70. *Istieus grandis* Agassiz. Neurocranium in dorsal view. Composite of several B.M.N.H. specimens.

relationships of the metapterygoid to the endopterygoid and ectopterygoid are similar to those in *Pterothrissus*. The ectopterygoid bears few teeth and these are considerably smaller than those on the endopterygoid or parasphenoid. The quadrate differs from that of *Pterothrissus* in being without a posteriorly directed spine. The palatine was cartilaginous and covered anteriorly by a small dermopalatine.

Dermal upper jaw. The upper jaw extends back to behind the level of the lateral ethmoid, in contrast to that of *Pterothrissus*. In shape and mode of articulation both the premaxilla and maxilla are similar to those in the Recent genus. However, the maxilla of *Istieus* bears more teeth and the single ovoid supramaxilla is relatively larger. The lateral surface of the premaxilla shows one or two small sensory pores.

Mandible. The lower jaw of *Istieus* is relatively longer than that of *Pterothrissus* and results in the mouth being sub-terminal instead of decidedly inferior. Other differences between the lower jaw of *Istieus* and *Pterothrissus* include : the position of the coronoid process which is situated posteriorly in *Istieus*, the relatively smaller size of the articular, and the size of the dentary teeth. In *Pterothrissus* the dentary teeth are needle-like and of the same size as those on the premaxilla. Those of *Istieus* are conical (it is admitted that the difference between conical and needle-like is relative rather than absolute), larger and more robust than the premaxillary teeth (Text-fig. 71).

Further features to be noted concerning the lower jaw of *Istieus* are the sites of ligament insertion. Immediately anterior to the articulatory cup the posterior margin of the articular is thickened for the insertion of the maxillary-mandibular ligament. Finally, the posterior face of the articular (that area which may be termed the retroarticular process, without the implication that a separate ossification is present) is pitted to receive the interopercular-mandibular ligament.

Circumorbital series. This series is poorly known. The condition of preservation makes it difficult to identify a supraorbital and the rostral ossicles, of which there were probably three, have become so displaced as to render interpretation of their spatial relationships impossible. The antorbital is a narrow splint-like element.

The infraorbital series is shown in Text-fig. 71. Although the suture lines between the separate elements are not distinct on any specimen an overall resemblance with *Pterothrissus* is evident. Certain minor differences occur : the first infraorbital of *Istieus grandis* is relatively smaller, less rounded and does not bear a dorsal prominence ; posteriorly, at the ‘ elbow ’ of the series, the margin is not produced in a process and the sensory canal appears to have lain entirely superficial to the fourth and fifth infraorbitals. These minor differences are overshadowed by the strong points of similarity such as the small dermosphenotic, which is more closely associated with the skull roof than with the other infraorbitals, the narrow posterior infraorbitals and the large rolled margin.

Opercular series. A comparison of Text-figs. 71 and 66 shows a close similarity between the constituent elements in *Istieus* and *Pterothrissus*. Two minor differences are apparent : the operculum of *Istieus* is smaller and the postero-ventral part of the preoperculum is less expanded. The anterior limb of the suboperculum of *Istieus* is smaller than in *Pterothrissus*.

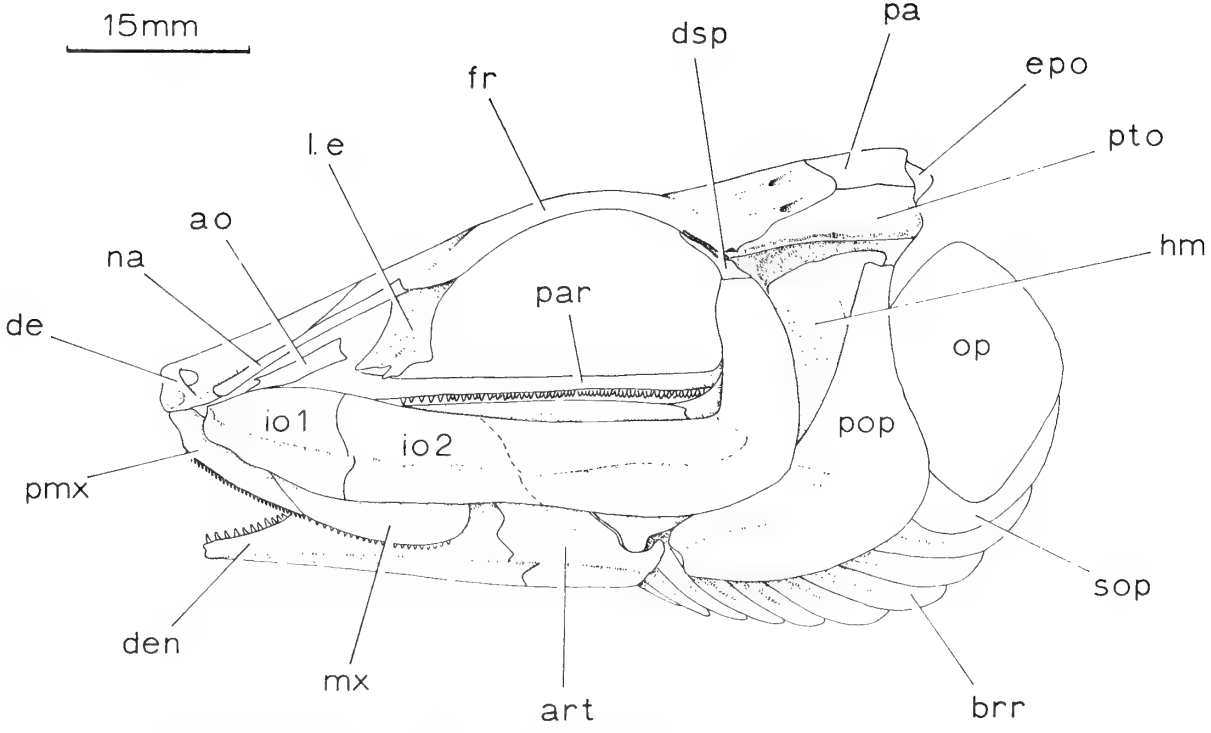

Fig. 71. *Istieus grandis* Agassiz. Cranium in left lateral view. Composite of several B.M.N.H specimens.

Cephalic sensory canal system. The sensory canals of the head were mainly contained within open troughs. A comparison of *Istieus* with *Pterothrissus* shows a similarity in basic design. On the skull roof the supraorbital canal of *Istieus* runs for a greater distance within the frontal, opening to the surface of the bone above the anterior half of the orbit. The otic sensory canal of *Istieus* is contained within a groove, the walls of which are more complete than in *Pterothrissus*.

Hyoid arch and branchiostegal rays. The anterior ceratohyal of *Istieus* is relatively longer than in *Pterothrissus* and this is reflected in a greater number of branchiostegal rays. 8–10 branchiostegals are present in *Istieus*, the upper (posterior) two being borne by the posterior ceratohyal. The variation in the number of branchiostegals affects those placed anteriorly.

Each branchiostegal is broad, curved and marked by a prominent ridge which expands proximally to form an articular head.

Postcranial skeleton. The impressions left by the pectoral girdle and fin are imperfect but the observable details are similar to comparable structures in *Pterothrissus*. The supratemporal is small and placed laterally, the cleithrum shows a posterior expansion above the area of fin insertion and the anterior portion of the cleithrum is narrow. The fin is composed of not less than 12 rays. In outline the fin is rounded distally. A pectoral splint is associated with the base of the outermost ray.

The pelvic girdle and fin are closely similar to those of *Pterothrissus*. The pelvic fin originates beneath the thirty-eighth to forty-second vertebra.

The vertebral count varies from 87 to 92 in the few specimens from which reasonably accurate counts could be made. The posterior 38–40 vertebrae are caudal, giving a caudal/total ratio of 48 per cent, a figure considerably higher than in *Pterothrissus gissu* in which this ratio is 32 per cent (*Istieus macrocephalus* has a caudal/total ratio of 40 per cent). Even though there are relatively more caudal vertebrae in *I. grandis*, the relative length of the caudal region is the same as in *Pterothrissus*, a discrepancy due to the majority of the caudal centra in *I. grandis* being shorter than the abdominal centra. *I. macrocephalus*, although having relatively fewer caudal vertebrae than *I. grandis*, shows a relatively longer caudal region than either *I. grandis* or *Pterothrissus*. The abdominal centra of *I. macrocephalus* are considerably shorter than the caudal centra, the reverse of the situation in *I. grandis*.

The morphology of the neural arches and spines, the haemal arches and spines, the parapophyses, pleural ribs, intermusculars and supraneurals is similar to that described for *Pterothrissus*. In some specimens of *Istieus* irregularly shaped ridges are seen passing upwards and backwards from the bases of the neural arches. These ridges are interpreted as the impressions left by tough myocommata, a feature noted in *Pterothrissus*.

Both the dorsal and anal fins are similar in shape, relative size and anatomy to those of *Pterothrissus*. The differences are merely those of meristic counts.

The caudal skeleton of *I. grandis* is similar to *Pterothrissus* as may be seen by comparing Text-figs. 72 and 68. The important points of similarity are : the ornamentation of the centra, the narrow neural and haemal spines, the two narrow uroneurals, the narrow hypurals with a large gap between the second and third, the

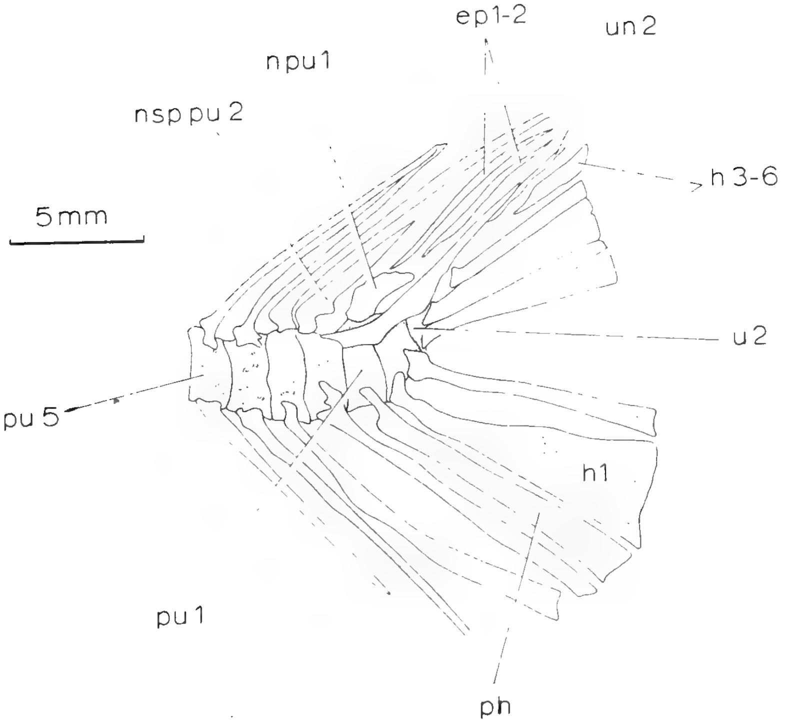

FIG. 72. *Istieus grandis* Agassiz. Caudal skeleton in left lateral view. Camera lucida drawing of B.M.N.H. 20586, fin-rays omitted.

unexpanded bases of the inner fin-rays and the unsegmented condition of nearly all the basal fulcra. Dissimilarities are also evident : *I. grandis* shows only two epurals (the caudal skeleton of *I. macrocephalus* is not known in this respect), the second uroneural is relatively smaller, the first uroneural extends forwards to reach the second preural centrum and there are more basal fulcra. In the specimen figured (Text-fig. 72) hypural four is partially fused to the fifth hypural.

Istieus macrocephalus Agassiz

(Text-fig. 74)

1833–44 *Istieus macrocephalus* Agassiz : **5**, pt 1, p. 13, pt 2, p. 93, pl. 16.
1863 ? *Istieus macrocephalus* Agassiz ; Marck : 39, pl. 4, fig. 6, pl. 5, fig. 3.
1901 *Istieus macrocephalus* Agassiz ; Woodward : 70.
1954 *Istieus grandis* Agassiz ; Siegfried : 11.

DIAGNOSIS (emended). *Istieus* reaching 250 mm S.L. Operculum twice as deep as wide. Six branchiostegal rays. Vertebral column with not more than 75 vertebrae. Dorsal fin with 41–44 rays. Body slender, with a narrow caudal peduncle.

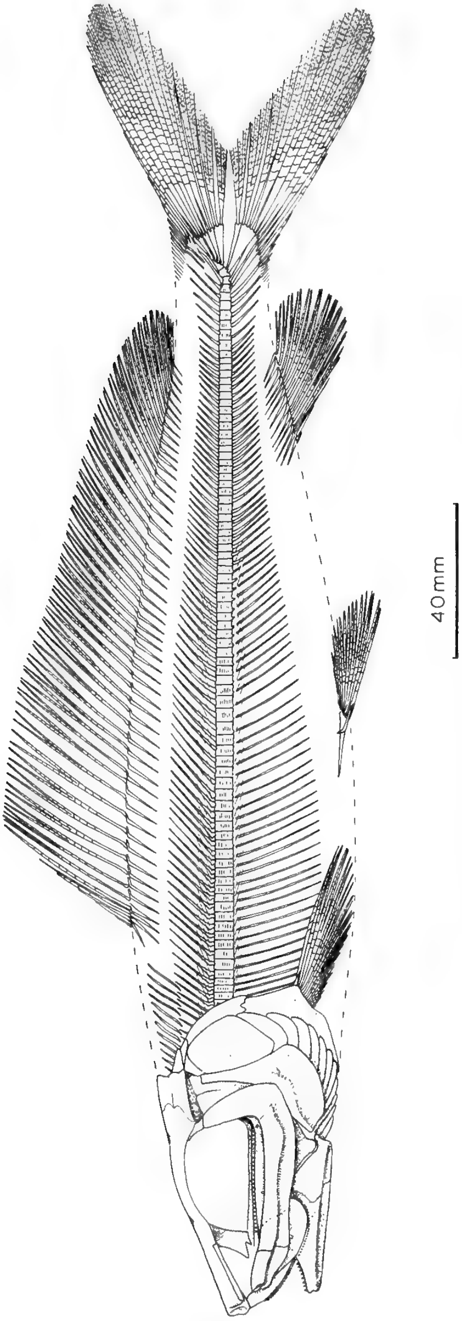

FIG. 73. *Istieus grandis* Agassiz. Entire skeleton, scales omitted.

Holotype. B.M.N.H. P.3892, a nearly complete fish exhibiting a dorso-ventrally crushed cranium and lacking part of the tail. From the Campanian of Baumberg, Westphalia, Germany.

Material. The holotype and B.M.N.H. 1275, a complete fish from the same locality as the holotype. The specimens are preserved in a buff-coloured limestone.

Remarks. Agassiz (1835) separated *I. macrocephalus* from other species of the genus on the basis of its larger head. This difference is more apparent than real. The head length in the type-species and *I. macrocephalus* is similar, 30–34 per cent of the standard length. The maximum depth of the head is also comparable. Marck (1858, 1863) also recognized a species *I. macrocephalus* and followed Agassiz in quoting the size of the head as the diagnostic character, but parenthetically it should be added that the figure of *I. macrocephalus* given by Marck (1863 : pl. 4, fig. 6) shows a dorsal fin-ray count unlike that of Agassiz's type specimen. Thus, *I. macrocephalus* described by Marck may not be that of Agassiz (1835).

Woodward (1901 : 71) recognized *I. macrocephalus* as a good species, but made no mention of head length. Instead he separated *I. macrocephalus* from the type-species on the basis that it had fewer dorsal and anal fin-rays, that the anal fin arises behind the dorsal and that the whole fish is of a more slender form.

The dorsal fin-ray count is decidedly lower (41–44 in *I. macrocephalus*, 53–57 in *I. grandis*) and the fish is more slender, a feature probably giving the mistaken impression of a larger head. In *I. macrocephalus* the body tapers more markedly to a narrower caudal peduncle than in *I. grandis*. Contrary to Woodward's opinion (1901 : 71) the anal fin actually arises in the same position relative to the dorsal fin and vertebrae in both species, as may be seen by a comparison of Text-figs. 73 and 74. The apparent posterior insertion of the anal fin in the type specimen of *I. macrocephalus* is due to the absence of the posterior dorsal fin-rays in the fossil.

Other differences include : the vertebral count, 87–92 in *I. grandis*, not more than 75 in *I. macrocephalus* ; the operculum of *I. macrocephalus* is narrower (depth : width ratio of this bone is 2 : 1 against 1·4 : 1 in the type-species) and has a more oblique ventral margin ; there are only 6 branchiostegals in *I. macrocephalus* against 8–10 in *I. grandis*. Finally, the snout appears more rounded in *I. macrocephalus*, but this may be due to distortion during preservation.

Thus, *I. macrocephalus* may be separated from the type-species on the shape of the operculum, the number of branchiostegal rays, dorsal fin-ray and vertebral counts and the caudal peduncle depth. The general trend in Pterothrissidae appears to be towards elongation of both the vertebral column and dorsal fin. In this respect *I. macrocephalus* is more primitive than *I. grandis* ; in contrast, the lower number of branchiostegal rays would suggest that *I. macrocephalus* is more specialized than *I. grandis*.

Remarks on other species

Two other species of *Istieus* have been described, *I. gracilis* Agassiz from the Campanian of Sendenhorst and *I. lebanonensis* Davis from the Upper Santonian of Sahel Alma in the Lebanon.

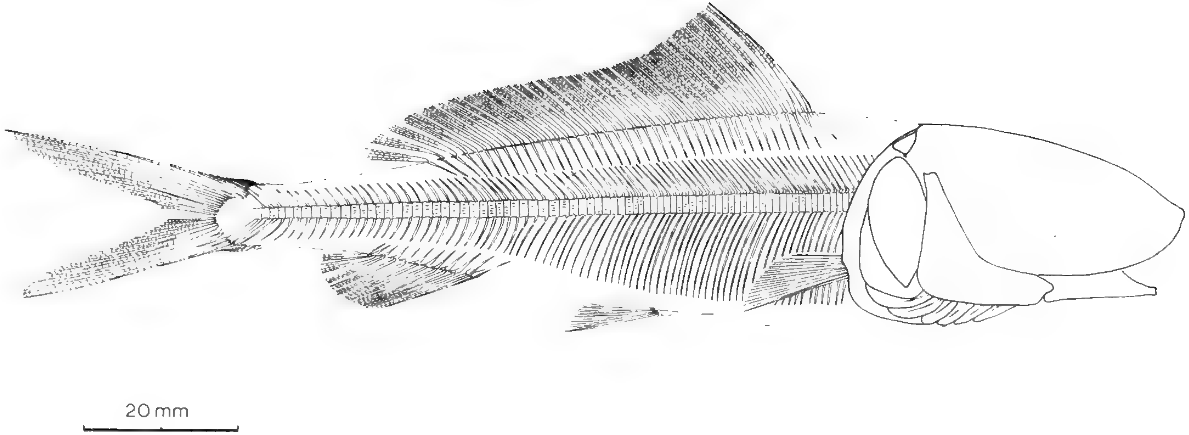

FIG. 74. *Istieus macrocephalus* Agassiz. Entire skeleton, scales omitted.

Istieus gracilis, so named because of the apparent slender form of this species, was considered by Woodward (1901) to represent specimens of *I. grandis* which had become distorted during preservation. I have examined neither the holotype nor many specimens which have been referred to this species. Two examples preserved in a single slab (B.M.N.H. P.3889), which were compared by Woodward (1901) to forms described as *I. gracilis*, show meristic counts similar to those of *I. grandis*. The evidence available to the author is not sufficient either to include the '*I. gracilis*' form with the type-species or to recognize a distinct species. Siegfried (1954 : 11) recognizes *I. gracilis* on the basis of the slender body form.

Istieus lebanonensis is known only from the holotype, which is poorly preserved. Little may usefully be added to the descriptions given by Davis (1887) and Woodward (1901). The size and dorsal fin-ray count are closer to those of *I. macrocephalus* than *I. grandis*.

Affinities of the genus *Istieus*

Istieus was placed by Agassiz (1833–44) in the family Esocoides as the only marine genus in an otherwise freshwater group of fishes. In establishing the genus Agassiz (*op. cit.*) recognized four species, *I. grandis*, *I. macrocephalus*, *I. gracilis* and *I. microcephalus*. With the exception of *I. macrocephalus* the descriptions and figures given by Agassiz do not justify separation at the species level.

Marck (1863) followed Agassiz, both with regard to familial placement and the recognition of several species, but he later (1873) combined *I. grandis* and *I. microcephalus* in a single species to which he gave the name *I. macrocoelius*. Such an action is contrary to the rules of nomenclature. Marck (1863) also established a new species, *I. mesospondylus*, which is here considered a synonym of the type-species.

Woodward (1901) recognized two species from Westphalia (*I. grandis* and *I. macrocephalus*) and another from Sahel Alma (*I. lebanonensis*). These are the only species recognized here. Woodward (1901) placed the genus in the Albulidae to which it is clearly related.

Istieus is very similar to the extant *Pterothrissus*, a view expressed by Woodward (1901) who stated that the two genera are not easily distinguished from one another. This similarity is endorsed by Greenwood *et al.* (1966) and Goody (1969b). Differences that do exist between the genera are minor. Many have been mentioned above in the description of *Istieus grandis*. The more important differences are mainly in degree, not absolute : thus *Istieus* shows a larger head ; a wider skull roof ; a more terminal mouth ; a smaller first infraorbital which reaches well forward ; more extensive parasphenoid teeth ; more teeth on the endopterygoid and (particularly) the ectopterygoid ; and finally more teeth on the maxilla. In all these respects *Istieus* may be considered more primitive than *Pterothrissus*. Absolute differences between the genera are few. *Istieus* shows a difference in tooth size between those teeth borne by the upper and lower jaws, a well-developed ridge upon the metapterygoid, two epurals and a posteriorly situated coronoid process. In contrast *Pterothrissus* has premaxillary and dentary teeth of equal size, no well-defined ridge on the metapterygoid, three epurals and an anteriorly situated coronoid process.

Except for the lower number of epurals and possibly the differentiation in tooth size, *Istieus* is the more primitive of the two genera. Both these features may not necessarily be of generic significance because the lower jaw dentition and the caudal skeleton of *I. macrocephalus* and *I. lebanonensis* are poorly known.

Apart from the differences mentioned above there are morphometric and meristic dissimilarities, but there appears to be as much intrageneric variation within *Istieus* as there are intergeneric differences between it and *Pterothrissus*.

The minor differences between *Istieus* and *Pterothrissus* are far outweighed by the many important features of similarity in neurocranial anatomy, the hyopalatine series, the infraorbital series, the dermal jaws, the form of the teeth, the cephalic sensory canal system and the fins (particularly details of the caudal skeleton).

The great similarity in form leads one to ask whether it would be advisable to regard *Istieus* and *Pterothrissus* as congeneric. Such a question can only be answered subjectively. Considered alone, none of the differences mentioned above would separate these forms at the generic level, but the nature and sum of the differences lead me to suppose that *Istieus* is markedly more primitive, to a degree that can only be appreciated by conferring generic status on the Cretaceous forms.

Genus ***HAJULIA*** Woodward, 1942

1942 *Hajulia* Woodward : 557.

DIAGNOSIS. See Woodward (*op. cit.*).

TYPE AND ONLY SPECIES. *Hajulia multidens* Woodward.

Hajulia multidens Woodward

1942 *Hajulia multidens* Woodward : 557, pl. 6, fig. 3.

DIAGNOSIS. See Woodward (*op. cit.*).

HOLOTYPE. Nearly complete fish, no. 100509 in the American University, Beirut, from the Middle Cenomanian of Hajula, Lebanon.

REMARKS. *Hajulia*, from the Middle Cenomanian of Hajula, was considered an albuloid by Woodward (1942) who suggested a relationship with *Istieus*.

The pterothrissid nature of *Hajulia* is indicated by the following features : the rounded trunk as evidenced by the presence of short, curved pleural ribs ; the shallow neurocranium which exhibits a slightly elongated snout ; the mouth which is slightly inferior, and the toothed maxilla which bears a single supramaxilla ; the palatal dentition in the form of large conical teeth on the parasphenoid, endopterygoid and possibly the basibranchium. The coronoid process is placed posteriorly, as in *Istieus*, and the quadrate/mandibular articulation lies beneath the posterior half of the orbit. There are less than 10 branchiostegals, although the exact number is not known.

Between the occiput and the dorsal fin there is a complete series of slender supraneurals. The dorsal fin itself is slightly elongated, situated in the centre of the back, and in profile resembles that of *Istieus* and *Pterothrissus*.

The caudal skeleton has six slender hypurals and a half neural spine on the second preural centrum. The neural and haemal spines are not expanded, in contrast to those in albulids. Preceding the upper and lower principal rays there is, as in *Istieus* and *Pterothrissus*, a series of very slender basal fulcra. Two B.M.N.H. specimens (P.13905 and P.13906), although reasonably well preserved in the caudal region, show no caudal scutes as recorded by Woodward (1942). In contrast to other pterothrissids, there are three uroneurals.

The vertebral column, with 50–55 vertebrae, is shorter than in other pterothrissids, but other features, although of a primitive nature, agree with this group. The anal fin is very short, consisting of only seven rays, unlike the longer anal fin of *Istieus and Pterothrissus*.

The pectoral girdle of *Hajulia*, with the fin inserted just beneath the level of the vertebral column, is unlike that of the pterothrissids. In this, and the shape of the ventral part of the cleithrum, there is a resemblance to the tselfatioids (*sensu* Patterson 1967c), but there is nothing else about *Hajulia* to suggest such an affinity.

The sum of these briefly noted morphological characters indicates that Woodward's (1942) suggested affinity of *Hajulia* was correct. However, incomplete knowledge of *Hajulia* precludes anything but a tentative assignment to the Pterothrissidae, and in consequence a fuller discussion of this genus is omitted.

Family **ALBULIDAE** Bleeker, 1859

Diagnosis. Albuloid fishes in which the snout is elongated, mouth inferior. Ethmoid commissure incomplete, running through premaxillae. Supraorbital sensory canal not extending onto parietal. Occipital condyle formed by basioccipital. Interorbital septum ossified. Lateral ethmoid sutured with broad parasphenoid. Parasphenoid and endopterygoid with a prominent crushing dentition opposed by similar dentition upon the basibranchial tooth plate. Basihyal tooth plate edentulous or absent. Vomer, dermopalatine, premaxilla and dentary with small needle-like teeth. Posterior infraorbitals broad, covering cheek. Supraorbital small. Hyomandibular-metapterygoid foramen present. Premaxilla tightly bound to mesethmoid; maxilla moving independently, a single supramaxilla. Mandible with low coronoid process situated posteriorly; articular and endosteal articular ossified separately. Branchiostegals more than 12 in number. Gular plate present. Dorsal and anal fins short based. Caudal skeleton with a full-length neural spine associated with the second preural centrum, two uroneurals. Inner caudal rays of each lobe without expanded bases. Caudal scute present above and below peduncle.

Genus ***ALBULA*** Scopoli, 1777

For synonymy see Hildebrand (1963).

Diagnosis (emended). Albulid fish in which the mouth is decidedly inferior, the maxilla is edentulous and extends to the anterior margin of the eye. Quadrate/mandibular articulation beneath anterior half of the orbit. Gular plate very small and disposed vertically. Vertebral column of 72–76 vertebrae. Caudal centra as long as deep and marked laterally by two grooves. Dorsal and anal fins without elongated terminal fin-ray. Caudal fin without fringing fulcra, preural neural spines expanded antero-posteriorly. Dorsal fin situated in the centre of the back. Anal fin nearer to the caudal peduncle than to the pelvic fin.

TYPE-SPECIES. *Esox vulpes* Linnaeus.

Albula vulpes (Linnaeus), 1758

(Text-figs. 75–84)

For synonymy see Hildebrand (1963).

DIAGNOSIS (emended). *Albula* in which the preorbital distance is considerably less than half the total neurocranial length. Quadrate/mandibular articulation beneath the lateral ethmoid. Parasphenoid, endopterygoid and basibranchial teeth of variable size, there being a decrease in average tooth size towards the edges of all tooth plates. Depth of neurocranium at the autosphenotic level equalling 26–28 per cent of the neurocranial length. Sub-epiotic fossae without ridges along the medial borders. Operculum slightly deeper than wide. Cranial roofing bones smooth. Dorsal fin with 17–19 rays, anal with 8–9.

HABITAT. All tropical and subtropical seas; in shallow water. Hildebrand (1963) gives a general account of *Albula vulpes* and refers to literature on the biology and ecology of the species.

REMARKS. *Albula vulpes* is often cited in literature. The descriptions of the cranium given by Ridewood (1904) and of the tail given by Hollister (1936) are particularly good. The comparative description given below is intended to supplement those works.

DESCRIPTION. *Neurocranium.* The relative dimensions of the neurocranium are similar to those of *Pterothrissus.* Thus it is long and shallow, the snout is narrow, the otic bullae are large, the subtemporal and sub-epiotic fossae are deep and the small post-temporal fossae are inclined antero-medially. As in all albulids the neurocranium is more heavily ossified than in *Pterothrissus.*

The skull roof (Text-fig. 75) shows several features commonly met with among albulids. The frontal is large with a deep trough anteriorly. Posteriorly the frontal reaches well back resulting in a small pterotic and parietal. The parietal is broader than long and of irregular shape. The nasal is large and in some specimens is ossified in two units, an anterior and posterior nasal ossicle.

The dermethmoid is of a more complicated shape than it is in pterothrissids. The dermethmoid of *A. vulpes* is raised to form a median ridge which, as in pterothrissids, is braced anteriorly by inclined struts. Anteriorly the dermethmoid ridge is widest dorsally where it shows a well-marked central groove that is covered in life by taut skin. Posteriorly the walls of this groove form ridges which pass postero-laterally and ' fade out ' on the frontals. At the point where the ridges

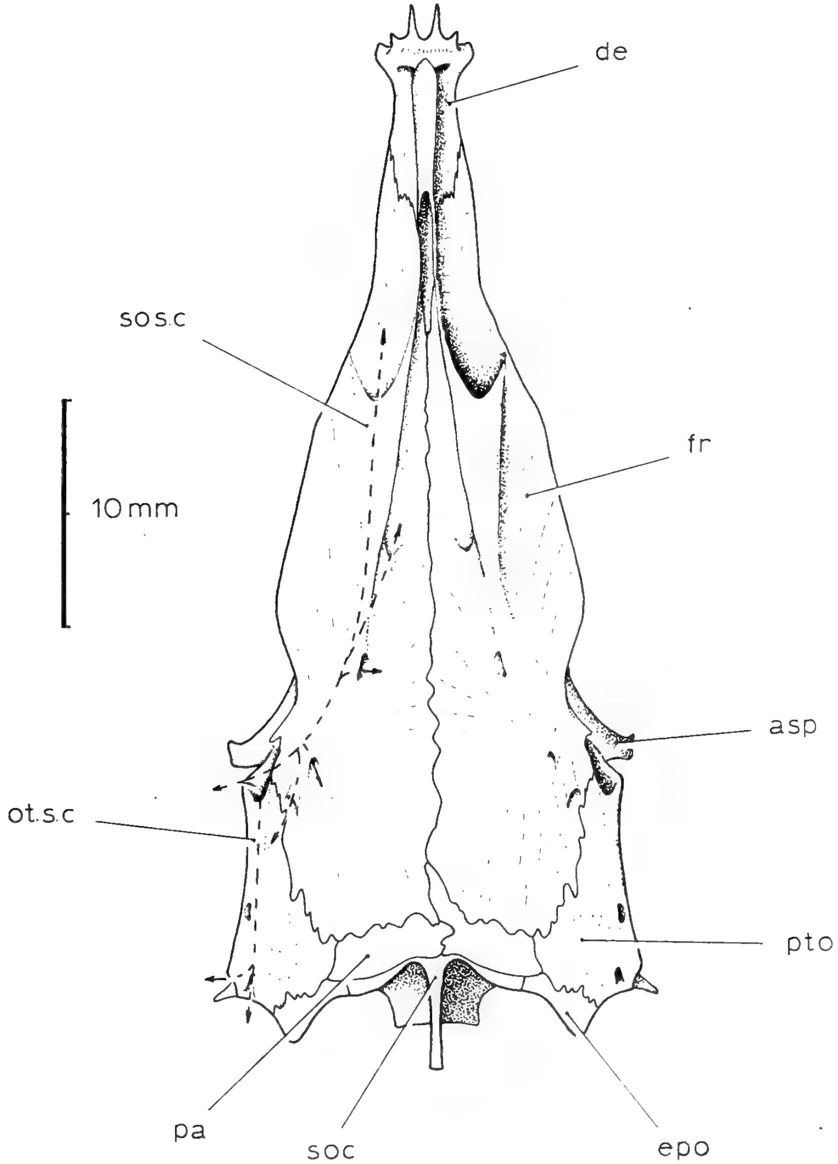

FIG. 75. *Albula vulpes* (Linnaeus). Neurocranium in dorsal view. Course of sensory canals shown by dotted line on left side. Composite of several B.M.N.H. specimens.

converge there is a deep, anteriorly directed pit which ends blindly within the body of the dermethmoid ridge. The ethmoid cartilage is ossified at its extreme anterior end in older individuals where perichondral bone surrounds spongy endochondral bone. Anteriorly the mesethmoid bears two articulatory facets set one above the other. Both facets are for articulation with the premaxilla. *Pterothrissus* has a single premaxillary facet.

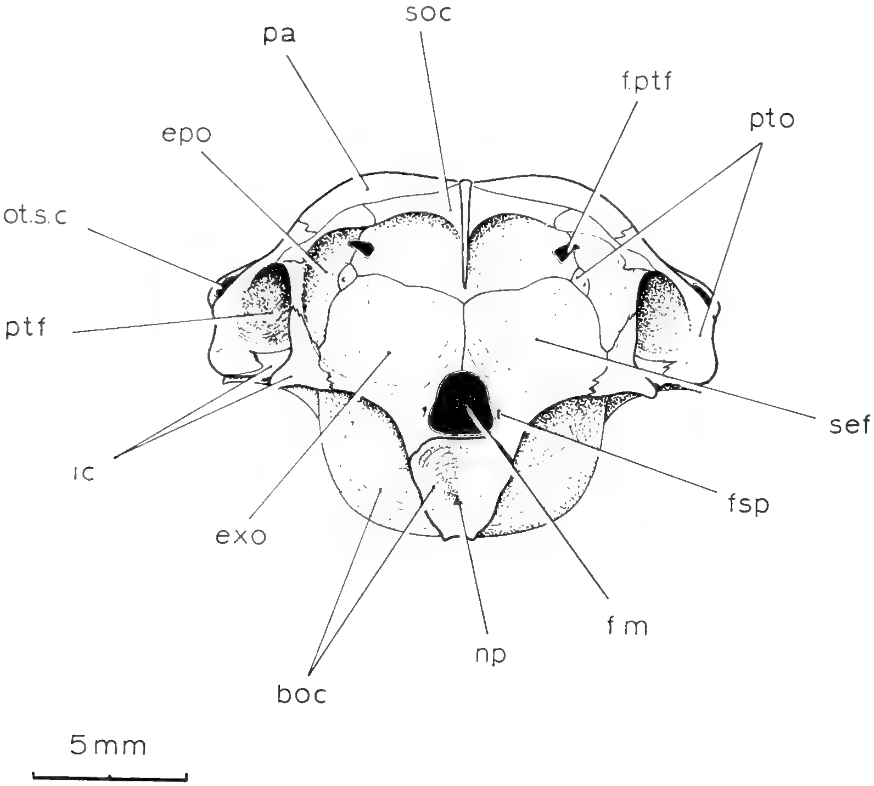

FIG. 76. *Albula vulpes* (Linnaeus). Neurocranium in posterior view. Composite of several B.M.N.H. specimens.

In posterior view (Text-fig. 76) the neurocranium shows large sub-epiotic fossae, small post-temporal fossae and large otic bullae. The supraoccipital is relatively larger than in *Pterothrissus,* due to its more extensive ossification. Two further features of interest in the posterior neurocranial wall of *A. vulpes* are the small 'isolated' portion of the pterotic and the foramen between the epiotic and supraoccipital. The 'isolated' portion of the pterotic represents the wall of the caecal end of the subtemporal fossa. Such a condition of the pterotic appears to be unique among lower teleosts, but in these the subtemporal fossa is rarely as deep, and even more rarely is it associated with a deep sub-epiotic fossa. The foramen between the supraoccipital and epiotic is occupied by epaxial musculature passing through to the post-temporal fossa.

The intercalar is small, as usual in albuloids, with little extension on the lateral face of the neurocranium. Posteriorly the surface of the intercalar bears ridges for the insertion of the tendon from the post-temporal.

The lateral neurocranial wall has in part been described by Ridewood (1904). Significant points are the depth of the roofed dilatator fossa ; the posteriorly placed opening of the jugular canal, close to the suture between the prootic and exoccipital ;

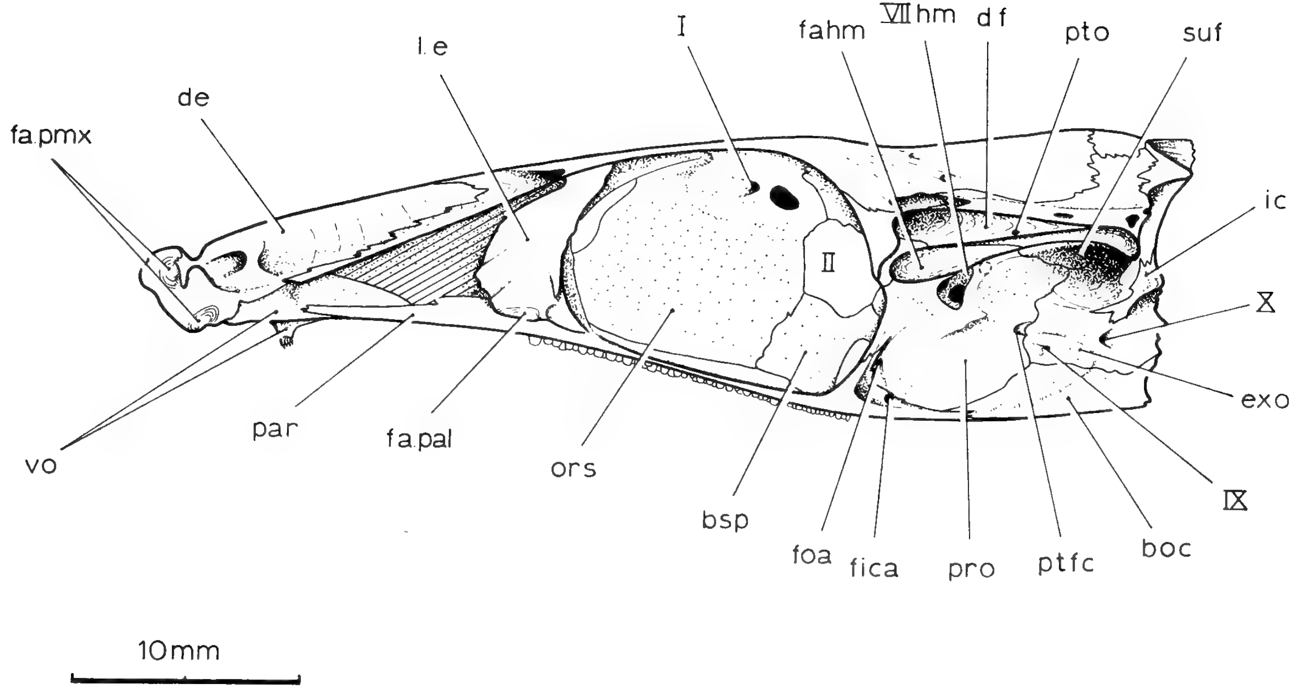

FIG. 77. *Albula vulpes* (Linnaeus). Neurocranium in left lateral view. Hatched area represents cartilage; dashed circle beneath *fahm* represents the position of a foramen seen in some specimens. From B.M.N.H. 1905.3.10.5.

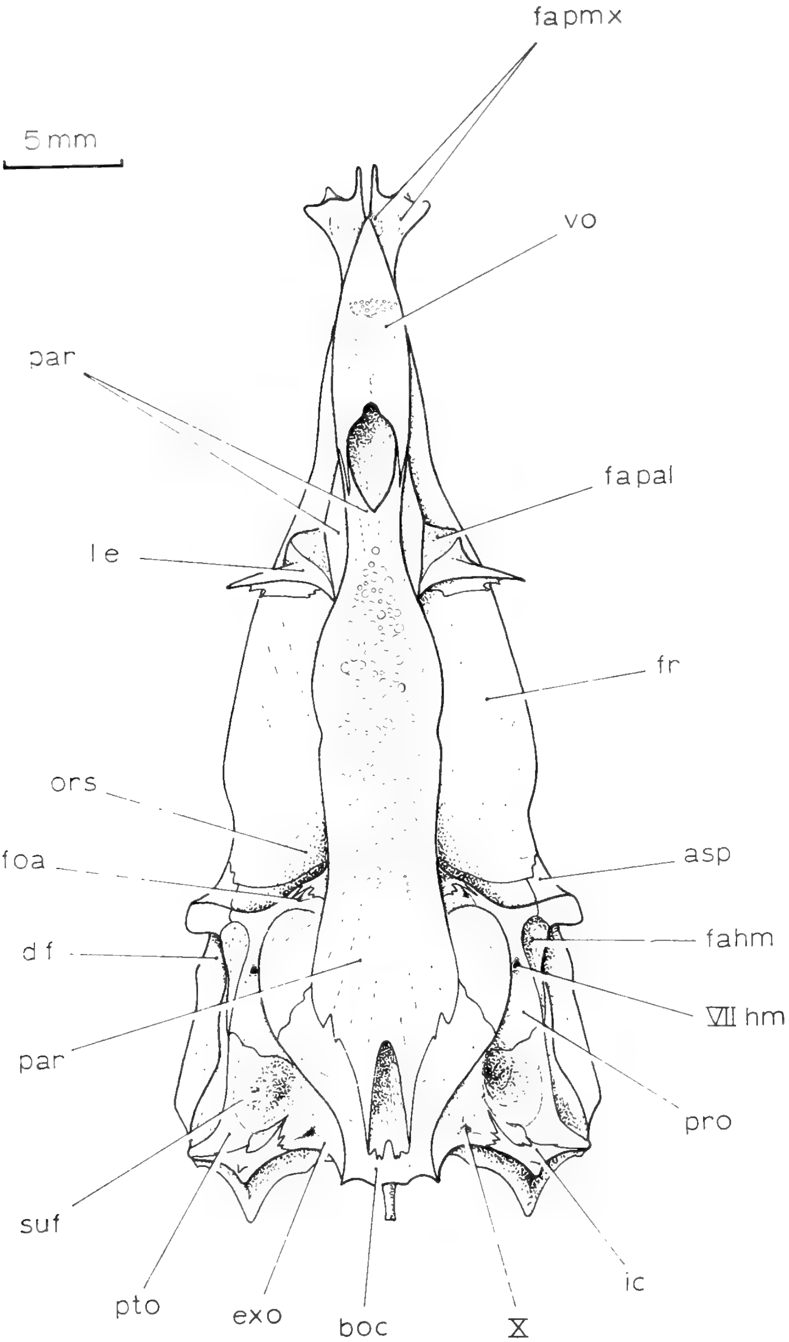

FIG. 78. *Albula vulpes* (Linnaeus). Neurocranium in ventral view. Composite of several B.M.N.H. specimens.

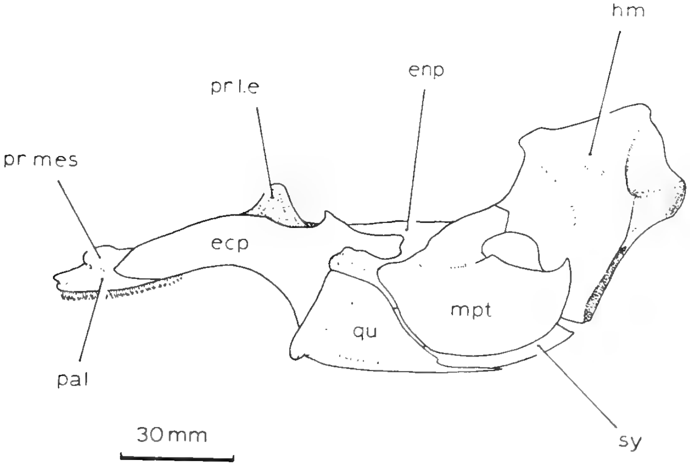

FIG. 79. *Albula vulpes* (Linnaeus). Hyopalatine series of left side in lateral view. Composite of several B.M.N.H. specimens.

the development of a ridge running antero-ventrally across the otic bulla from beneath the hyomandibular foramen, providing an anchorage point for branchial musculature; and the deep excavation at the base of the ascending process of the parasphenoid. This excavation is seen in other albuloid fishes although its significance is by no means clear. Postero-dorsally to the opening for the hyomandibular trunk there is often seen in large specimens (e.g. B.M.N.H. 83.12.15.106) a foramen which leads directly to the cranial cavity. Since this foramen is not a constant feature it cannot be of any great significance.

Within the orbit *Albula* shows a completely ossified interorbital septum which is sutured with a greatly expanded basisphenoid stem. Anteriorly the lateral ethmoid is large and stout, totally unlike that element in pterothrissids. Ventrally the lateral ethmoid is sutured with a thin lateral wing of the parasphenoid. The lateral ethmoid also bears a rounded articulatory area which articulates with the posterior process of the palatine.

The parasphenoid is wide throughout much of its length and bears many hemispherical teeth. Each parasphenoid tooth is smooth. The tooth size varies considerably throughout the toothed area but generally those teeth towards the rear of the patch are substantially smaller than those anteriorly. The vomer bears three or four rows of needle-like teeth which are inserted on a short pedicel.

Hyopalatine bones. The hyopalatine series is very much like that of *Pterothrissus*. The series is long and shallow; the hyomandibular slopes forward and between it and the metapterygoid there is a large foramen; the quadrate shows a posterior spinous process and the ventral margin lies almost horizontally; the symplectic is flattened and lies against both the metapterygoid and quadrate; the autopalatine is long and overlies much of the ectopterygoid.

The palatine remains largely cartilaginous, except in larger individuals. Two processes of the palatine begin to ossify early; anteriorly there is a rounded ethmoid

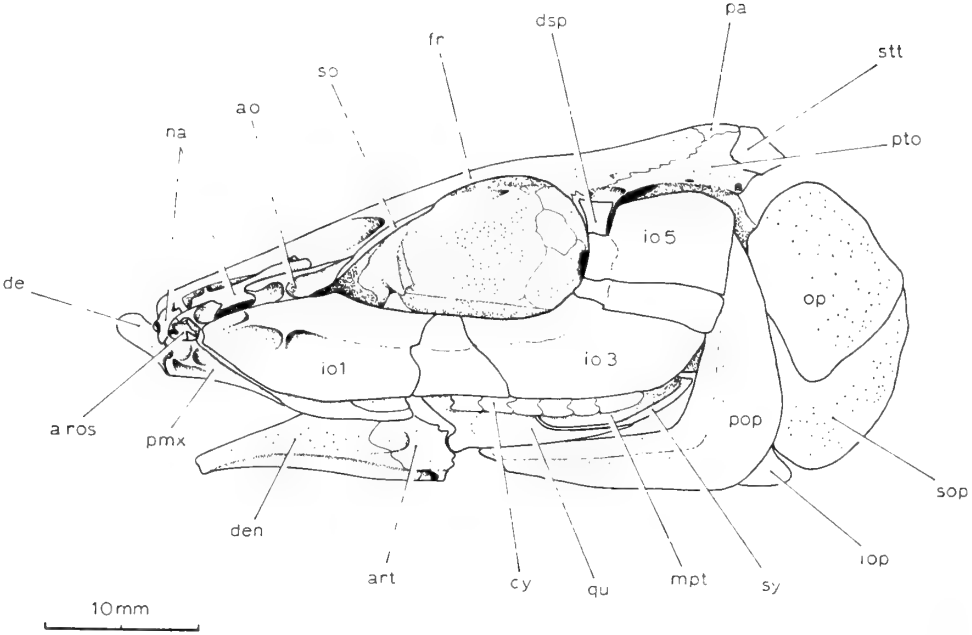

FIG. 80. *Albula vulpes* (Linnaeus). Cranium in left lateral view. Composite of several B.M.N.H. specimens.

process articulating with the mesethmoid ; posteriorly there is a large posterior (lateral ethmoid) process. The precocious ossification of these processes should not be interpreted as two embryonic divisions as Ridewood (1904 : 51) implied. Rather, these processes ossify early in response to a functional need. The dermopalatine is larger than in pterothrissids and carries many more teeth. The ectopterygoid is relatively large (cf. *Pterothrissus*) and bears a well-developed process upon its lateral surface. Ridewood (1904 : 51) reports the presence of a few ectopterygoid teeth but I have seen no example with teeth. The dentition of the endopterygoid is similar to that on the parasphenoid.

Dermal upper jaw. The upper jaw is formed by the premaxilla and the maxilla, the latter taking little part in the functioning of the jaw. The premaxilla bears on its outer surface a series of struts which form an incomplete outer wall to the premaxillary sensory canal. Anteriorly the premaxilla articulates with the ethmoid region by two medially directed heads, one above the other. Such a double articulation is not found in other albuloids and probably arose by a subdivision of a single elongate facet like that in *Pterothrissus*. The double articulation makes union with the ethmoid very strong and virtually immovable. The oral border of the premaxilla bears a band of fine, pointed teeth.

The edentulous maxilla is narrow anteriorly, but deepens posteriorly where it is partially overlapped by a single supramaxilla. The anterior end of the maxilla is turned inwards and is slightly swollen where it forms two rounded prominences.

The dorsal prominence probably corresponds to the palatine projection seen in elopoids and osmeroidids ; the ventral projection corresponds to the maxillary head. The maxilla is capable of moving independently of the premaxilla.

Mandible. The mandible is short, with a deep coronoid process situated posteriorly and a narrow symphysis. Both the endosteal articular and the sesamoid articular are large. The mandibular sensory canal is contained within a deep trough on the dentary and dermarticular. The dentition consists of a band of fine needle-like teeth on the dentary.

Circumorbital series. The supraorbital and antorbital are slender and form a thin strut, as in *Pterothrissus*. Two rostral ossicles lie anterior to the first infraorbital and as in other elopiforms are barely larger than the contained sensory canal.

The infraorbital series of *Albula* is typical of that of other albulids but differs somewhat from that series in the Pterothrissidae. The posterior infraorbitals are wide and completely cover the cheek region. The dermosphenotic is large, its posterior margin continuing that of the fifth infraorbital. As in *Pterothrissus* the infraorbital margin is rolled, but in *A. vulpes* the sensory canal is better protected by bone (cf. Text-figs. 80 and 66).

Cephalic sensory canal system. The system of canals upon the head is mainly contained in large troughs. The supraorbital canal runs within the frontal from the level of the autosphenotic to the level of the lateral ethmoid. Anterior to this the canal continues in the frontal trough and the nasal ossicle(s) to end blindly anteriorly. Gosline (1961) records a single median cavity separated from the supraorbital canal of either side by membrane. The epithelium lining this cavity appears to be supplied by a fine branch of the facial nerve and could therefore be related to the supraorbital canal.

The otic division of the cephalic sensory canal runs within the pterotic parallel to its dorso-lateral edge. The canal opens posteriorly by two pores, one directed laterally and joining with the preopercular canal, the other directed posteriorly and receiving the supratemporal commissure and the lateral line. Innervation of the otic canal is from two sources : anteriorly the otic branch of the facial pierces the autosphenotic, and posteriorly a supratemporal branch of the vagus pierces the lateral wall of the dilatator fossa.

The lateral portion of the supratemporal commissure is contained within the supratemporal while the middle section lies in the skin. Neither the pterotic nor the parietal is grooved, as they are in *Pterothrissus*.

Hyoid arch, gill arches and gular plate. The ceratohyal consists of a stout posterior element and a longer but narrower anterior element. The latter bears a deep groove on the lateral surface for the reception of branchiostegal rays. The afferent hyoidean artery does not pierce either hypohyal ; instead it passes upwards within the ceratohyal and runs back along a groove on the dorsal edge of the anterior ceratohyal. Of the 15 branchiostegal rays, the anterior three lie free in the branchiostegal membrane.

The gill arches are very similar to those of *Pterothrissus*. Minor differences that do exist concern the teeth borne by the basibranchial tooth plate. In *Albula vulpes* these teeth are hemispherical, irregular in size and show no pattern of size distribution. A basihyal tooth plate is absent.

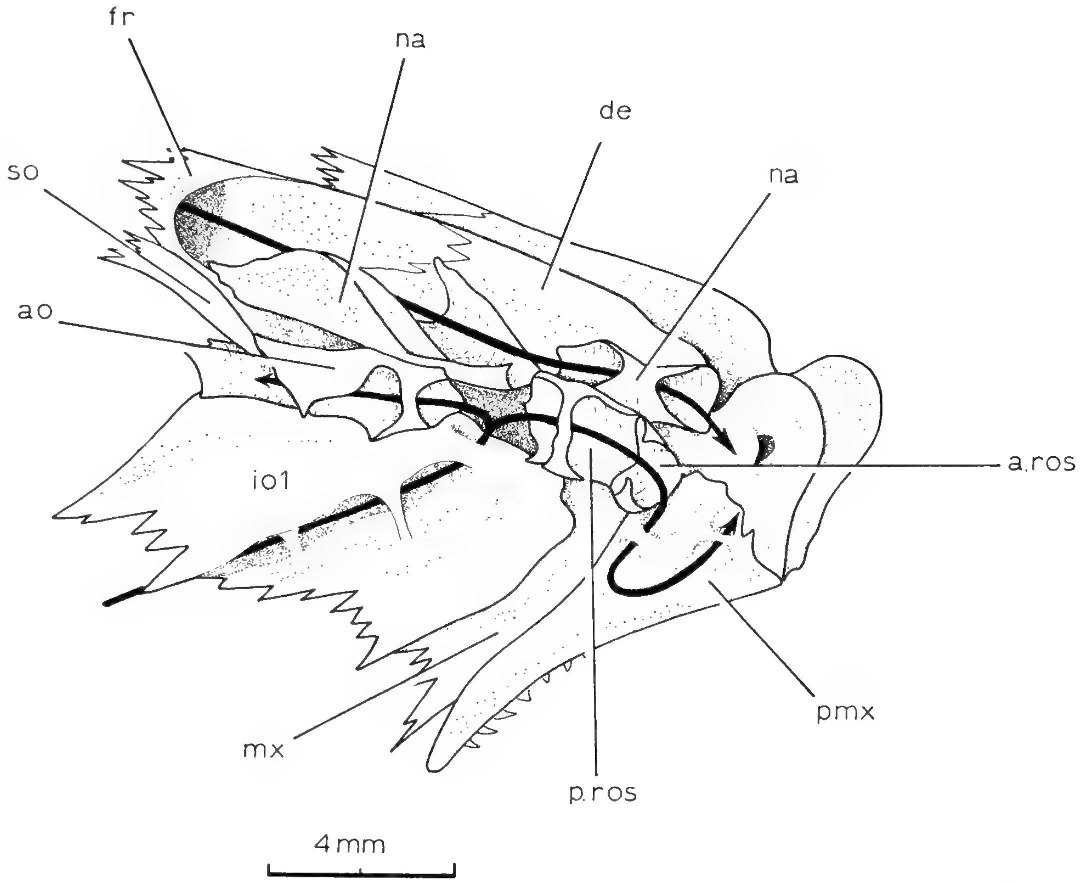

Fig. 81. *Albula vulpes* (Linnaeus). Anterior end of snout, circumorbital series and upper jaw in right antero-lateral and slightly superior view. The course of the supraorbital and infraorbital sensory canals is shown, arrow heads mark the termination of the canals. From B.M.N.H. 1905.3.20.5.

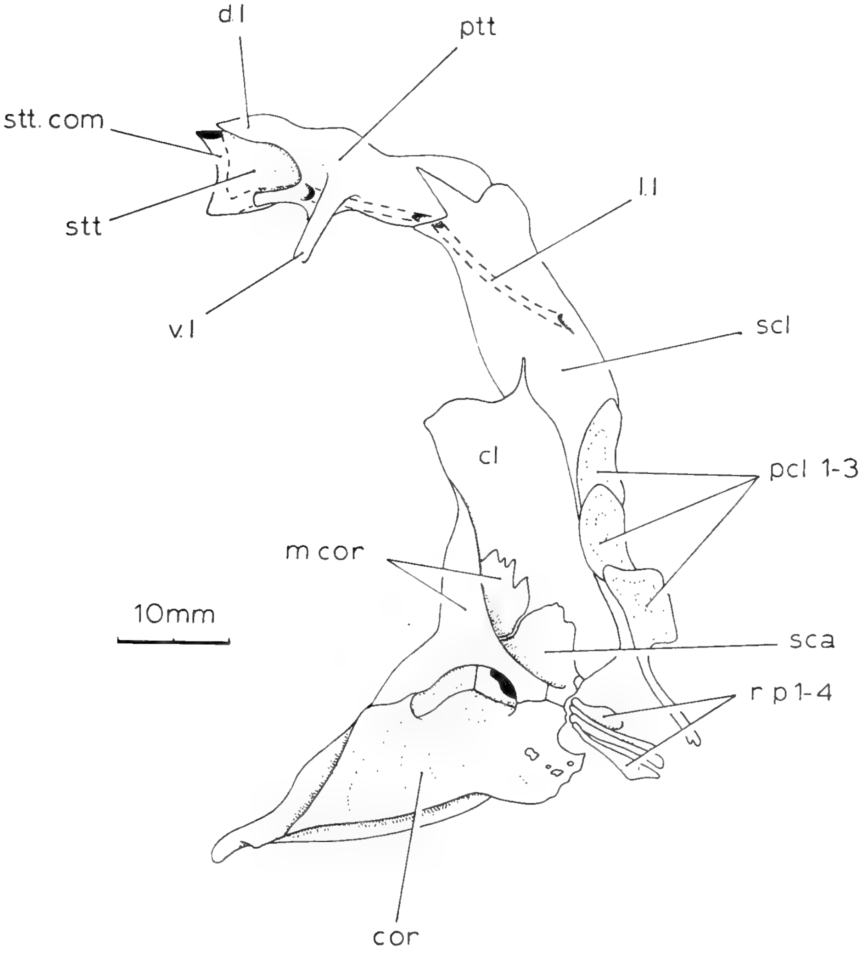

Fig. 82. *Albula vulpes* (Linnaeus). Pectoral girdle of right side in medial view. Composite of several B.M.N.H. specimens.

A small gular plate is seen in some specimens (Nybelin 1960), notably the larger individuals. Unlike the gular plate of other albuloids that of *A. vulpes* is vertical.

Paired fins. All bones composing the pectoral girdle (Text-fig. 82) are stout. The main body of the post-temporal is longer than wide and is produced into three processes, an epiotic (dorsal) limb, an intercalar (ventral) limb and a third limb which projects into the lumen of the post-temporal fossa and is embedded within epaxial musculature. The supracleithrum is the usual elongate element.

Many features of the ventral parts of the pectoral girdle are similar to those of *Pterothrissus*. The cleithrum is broad above the fin insertion but becomes narrow antero-ventrally ; the coracoid does not extend to the tip of the cleithrum ; an interosseous foramen is absent (in *Pterothrissus* it is very small) ; the scapula fails completely to enclose the scapular foramen ; and, finally, the anterior edge of the mesocoracoid fits tightly against the inflected margin of the cleithrum. The ventral end of the mesocoracoid is bifurcated, producing a foramen between the mesocoracoid and the coracoid. As in other parts of the skeleton the pectoral girdle of *A. vulpes* is more extensively ossified than that of *Pterothrissus*.

There are three postcleithra, the lowermost having a characteristic shape (Text-fig. 82).

The disposition, size and shape of the pectoral radials is similar to that described for *Pterothrissus*. There are 16–17 pectoral fin-rays of which all except the outermost are branched. A triangular pectoral splint is associated with the outermost ray.

The pelvic fin arises beneath the posterior half of the dorsal fin and is supported by a triangular pelvic bone. Anteriorly the pelvic bone is thin, but posteriorly it becomes considerably thicker and the hind margin is capped by cartilage with which the pelvic rays articulate. Medially, the base of the pelvic bone is produced as an ' ischial process '. There are 10 pelvic fin-rays, the outermost unbranched. Associated with the upper half of the first ray is a long splint bone, the proximal end of which is curved sharply upwards. Whitehead (1963 : 744, fig. 3a) shows the pelvic splint to be a double structure composed of an upper and lower portion. I could not find any convincing example of such a double structure in any B.M.N.H. specimen.

Median fins. The dorsal is situated nearer to the occiput than to the caudal peduncle and is composed of 17–18 rays, the anterior five of which are unbranched. The fin is supported by 15–16 pterygiophores. In older specimens successive pterygiophores appear to be fused distally.

The small anal fin is remote and composed of nine rays (occasionally eight) supported upon seven pterygiophores. Like the pterygiophores of the dorsal fin, the distal extremities may become fused in older specimens.

Vertebral column. The only complete vertebral count available to me (B.M.N.H. 83.12.15.106) showed 67 vertebrae of which 23 are caudal. Hildebrand (1963 : 134) gives the range of vertebral counts for the western North Atlantic forms as 72–74. All centra except the first 17 are as deep as long, the exceptional centra being deeper than long. Each centrum is marked laterally by a stout horizontal bar flanked by deep grooves. The centra bear deep pits dorsally and ventrally for the reception of neural arches and parapophyses or haemal arches respectively.

The bases of the neural arches are produced anteriorly and posteriorly forming small zygapophyses. The first 31 neural arches and spines remain distinct from their fellows of the opposite side and bear separate neural spines. Thus these vertebrae show a double neural spine.

The parapophyses of the first 44 centra show an elongate area which is inclined antero-ventrally and serves, with a facet on the centrum, for the articulation of the pleural rib. The posterior 12 parapophyses gradually increase in length and support a series of progressively shorter pleural ribs.

The neural and haemal spines of the caudal region are short. Those associated with the posterior centra are expanded in the sagittal plane and aid in supporting the caudal fin-rays. Preceding the first dorsal pterygiophore there is a series of

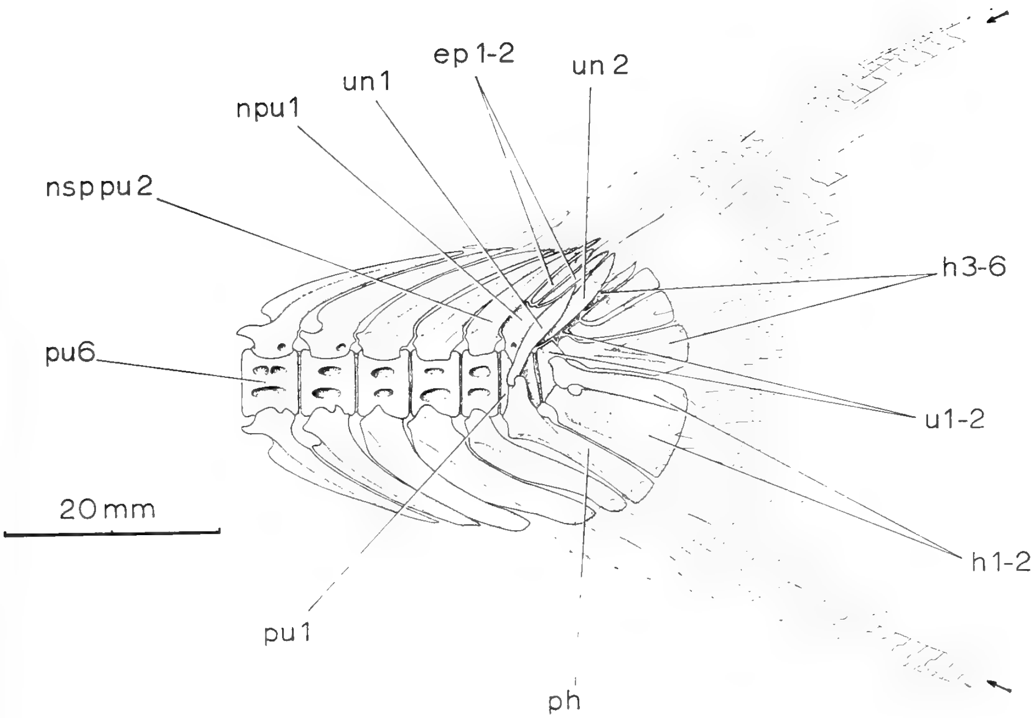

FIG. 83. *Albula vulpes* (Linnaeus). Caudal skeleton in left lateral view. Arrows indicate upper and lower principal fin-rays. Composite of several specimens.

supraneurals. Each is sigmoid in shape, with the anterior ones considerably stouter than the posterior members of the series.

Epineural intermuscular bones are borne by the neural arches throughout most of the abdominal and caudal regions. Epipleurals are found in the posterior abdominal region and grade posteriorly into a ventral series found throughout the caudal region.

Squamation. Lateral line scale counts vary considerably. Specimens from both coasts of Central America give counts ranging from 71–77. Hildebrand (1963 : 134), who based his counts on specimens from the western North Atlantic, records a range of 65–67. It may be mentioned here that an Aden specimen (B.M.N.H. 1962.3.26.9) also differs from the western Atlantic and eastern Pacific specimens in having 19 dorsal fin-rays. Hildebrand (1963) observed that only occasionally do Atlantic specimens show such a high count. Regrettably the dorsal fin of a Seychelles specimen was broken and accurate counts could not be made.

The branchiostegal ray count also varies with respect to geographical distribution (McAllister 1968 : 37) being higher in fishes from India and the Indo-Australian Archipelago. These biometrical differences may justify the recognition of a second Recent species.

Returning to squamation, the transverse count immediately anterior to the dorsal fin is eight above and nine below the lateral line row, excluding a median row of small

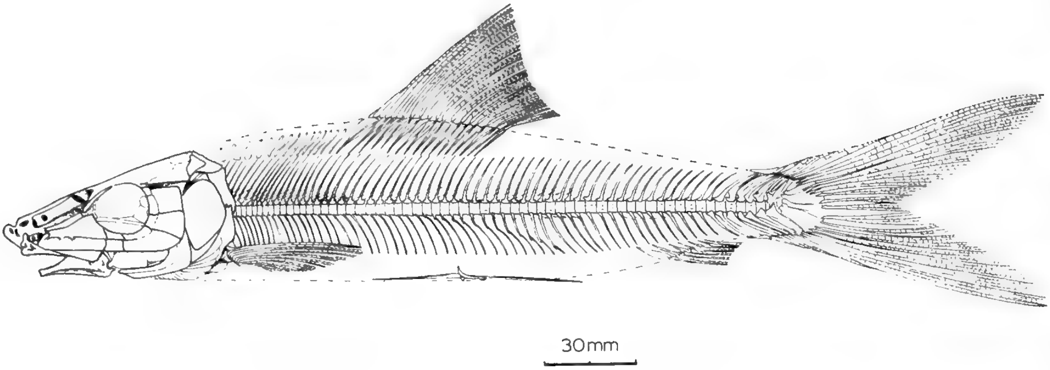

FIG. 84. *Albula vulpes* (Linnaeus). Entire skeleton, scales omitted.

scales which extends from the occiput to just behind the dorsal fin. The general body squamation consists of thin cycloid scales, more or less square in shape, with three to four basal radii and four to five basal lobes. The posterior edge of the exposed field is often broken due to the thinness of the scale. The surface of the scale is marked only by circuli.

The modified scale row in the mid-dorsal line consists of oval scales, whose length considerably exceeds their width. The bases of all fins are covered by scales. Axillary scales are present at the bases of the pectoral and pelvic fins. Bone cells are present in the scales.

Albula oweni (Owen)

(Text-figs. 85–87)

1840 *Pisodus owenii* Owen : 138, pl. 47, fig. 3.
1844 *Pisodus owenii* Owen ; Agassiz : **2**, pt 2, p. 247 (name only).
1854 *Pisodus owenii* Owen ; Owen : 167.
1891 *Pisodus oweni* Owen ; Woodward : 108, pl. 3, figs. 3–5.
1893 *Pisodus oweni* Owen ; Woodward : 357, pl. 17.
1901 *Albula oweni* (Owen) Woodward : 60, pl. 4, figs. 1, 2.
1908 ? *Albula oweni* (Owen) ; Priem : 82, fig. 38, pl. 4, fig. 12.
1946 *Albula oweni* (Owen) ; Casier : 122, pl. 3, fig. 12.
1952 *Albula oweni* (Owen) ; Arambourg : 242, pl. 37, figs. 1–6.
1966 *Albula oweni* (Owen) ; Casier : 133, pl. 13, fig. 4.

DIAGNOSIS (emended). *Albula* in which the preorbital part of the neurocranium is equal to half the total neurocranial length. Quadrate/mandibular articulation in advance of the level of the lateral ethmoid. Parasphenoid teeth of the same size throughout the toothed area. Depth of the neurocranium at the autosphenotic approximately 35 per cent of the neurocranial length. Opercular bone twice as deep as wide. Ornamentation in the form of coarse rugosities present on the lateral edges of the frontals above the orbit and on the quadrate.

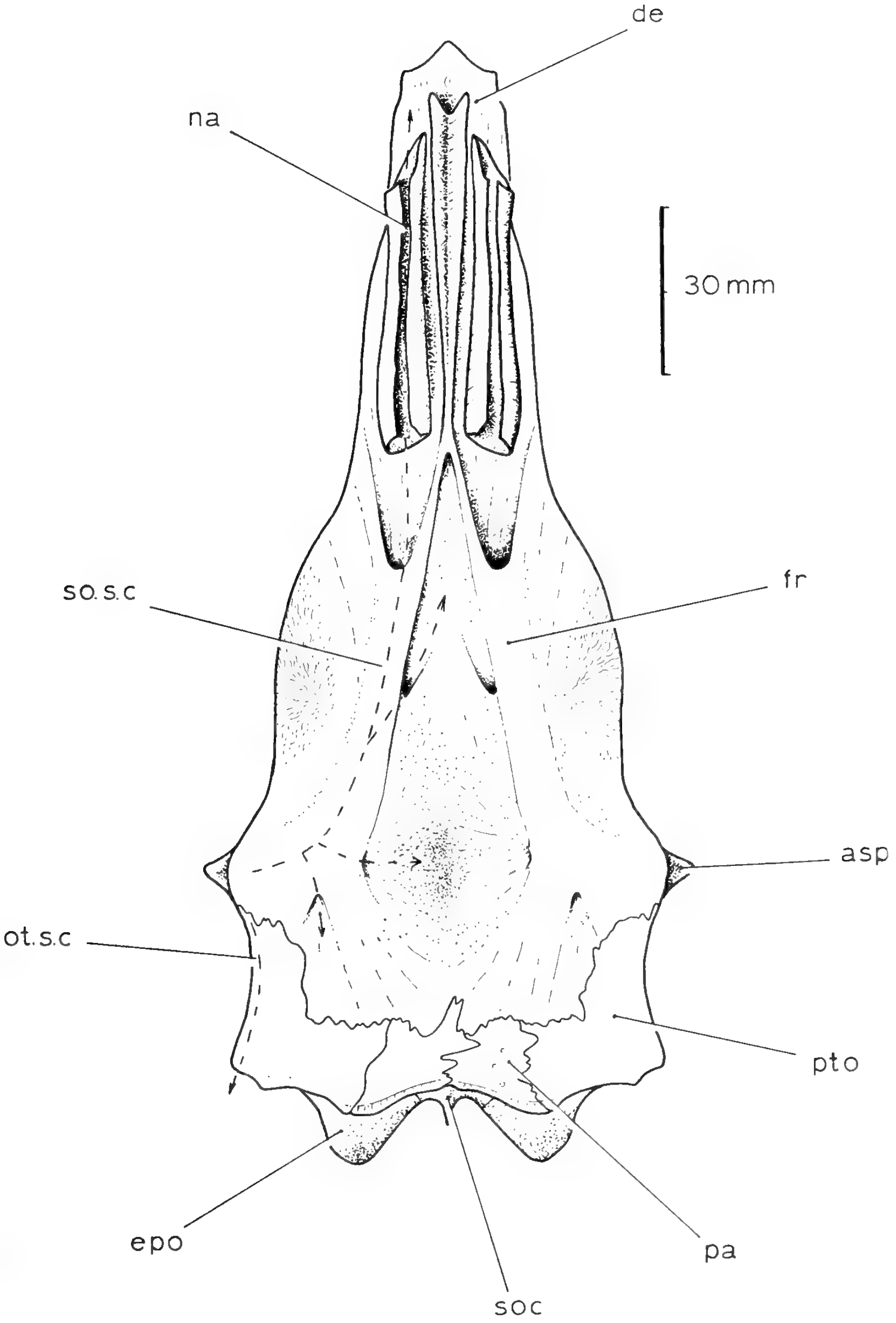

FIG. 85. *Albula oweni* (Owen). Neurocranium in dorsal view. Course of sensory canals shown by dotted line on left side. Based on B.M.N.H. 39439.

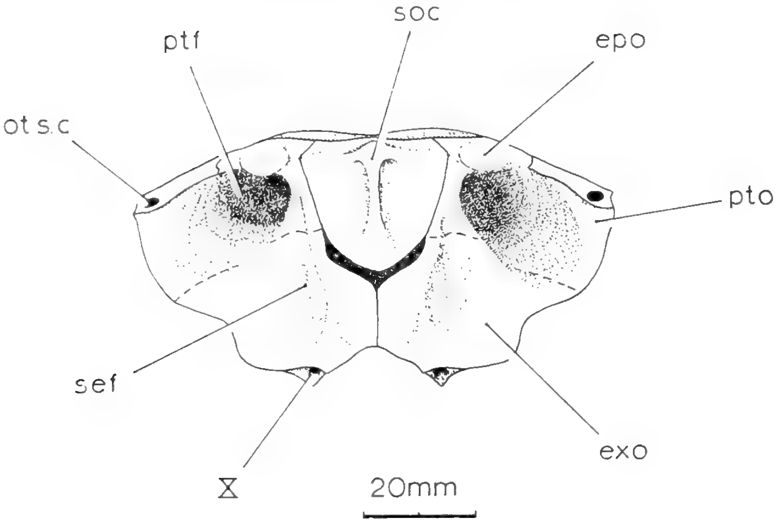

FIG. 86. *Albula oweni* (Owen). Neurocranium, posterior view of dorsal half. From B.M.N.H. 39439.

HOLOTYPE. Parasphenoid; in the collection of the Royal College of Surgeons, London. From the London Clay (Ypresian) of Sheppey, Kent, England.

MATERIAL. B.M.N.H. 39439, P.9158, and various isolated teeth, teeth with supporting bones, and a decaying specimen of the viscerocranium, all from the London Clay (Ypresian) of Sheppey. Postcranial remains are unknown.

HORIZON AND LOCALITY. Lower Eocene of S.E. England, France, Belgium and N. Africa, and Middle Eocene of Belgium.

DESCRIPTIVE REMARKS. Woodward (1901) distinguished *A. oweni* from *A. vulpes* by the relative lengths of snout to frontal notch in the two species. The frontal notch in *Albula* occurs at the hind margin of the lateral ethmoid and is thus comparable with the preorbital distance, a feature used here.

Several other neurocranial features distinguish *A. oweni* from the type-species.

In dorsal view the skull roof of *A. oweni* shows a marked median frontal depression at the level of the autosphenotic spine. Such a depression is suggested in *A. vulpes*, but it never attains the same relative proportions. Perhaps its development is a consequence of absolute size, this being greater in *A. oweni*. Above the orbit, the frontals exhibit a rugose ornamentation not seen in the extant species. Such ornament is seen in the Osmeroididae where it is often (*Osmeroides lewesiensis*) more extensive. Apart from these minor differences the skull roof of *A. oweni* (Text-fig. 85) is very similar to that of *A. vulpes* (Text-fig. 75).

The posterior neurocranial wall shows well-developed sub-epiotic fossae (an albuloid feature) which are bordered medially by stout vertical ridges (a feature typical of the osmeroidids but not found in *A. vulpes*). The supraoccipital of *A. oweni* (Text-fig. 86) is of different proportions to that of *A. vulpes* and there is a small interspace between the supraoccipital and exoccipitals. Neither an 'isolated portion ' of the pterotic (p. 156) nor a foramen between the supraoccipital and epiotic could be identified in *A. oweni.*

The depth of the neurocranium at the autosphenotic spine is relatively greater in *A. oweni* than in *A. vulpes*. The lateral neurocranial wall of *A. oweni* is incompletely known from a single specimen, and comparison with the extant species is difficult as features of individual variation cannot be taken into account. However, a few remarks are necessary.

The region which is occupied by the saccular swelling in *A. vulpes* is depressed and perhaps represents the point to which an arm of the swimbladder reached. In *A. vulpes* the swimbladder diverticulum, although of variable development (Greenwood 1970a), never reaches as far forwards as this point.

The subtemporal fossa of *A. oweni* is considerably larger than in *A. vulpes* and a horizontal ridge forms its ventral border. In *A. vulpes* no such ridge exists.

The posterior opening of the jugular canal (pars jugularis) lies, as usual, within the prootic bone, but in *A. oweni* the opening is situated far forwards, whereas in *A. vulpes* it is close to the posterior margin of the prootic. The specimen of *A. oweni* shows a lateral bridge of bone spanning the jugular groove behind the posterior opening of the pars jugularis. A greater anterior development of this lateral bridge would eventually meet the lateral commissure and produce the same spatial relationship of the posterior opening of the jugular canal as in *A. vulpes*. This development of a bridge, which may otherwise be thought of as a fenestrated lateral commissure, is in all probability subject to individual variation.

Lying antero-ventral to the posterior opening of the pars jugularis is a large postero-ventrally directed boss ; in the type-species there is only a stout ridge. The

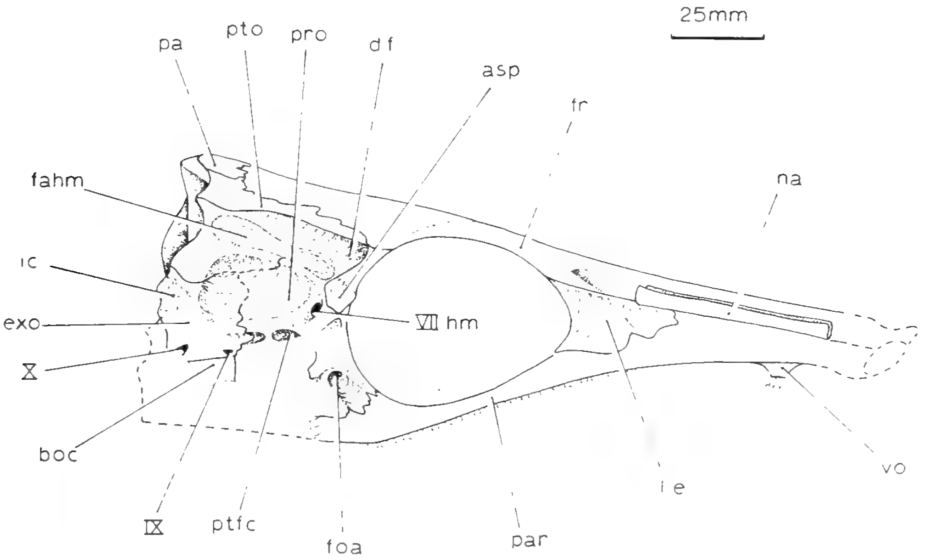

FIG. 87. *Albula oweni* (Owen). Neurocranium in right lateral view. Based on B.M.N.H. P.9158 and 39439.

tip of this boss in the prepared specimen (B.M.N.H. 39439) is spongy, suggesting that it was capped by cartilage. This boss probably received branchial musculature, as does the corresponding ridge in *A. vulpes*.

The dentition on the parasphenoid and vomer is very similar in both species, yet there are small differences. The parasphenoid teeth of *A. vulpes* show a gradation in average size from large anteriorly to smaller posteriorly where they also become more conical in shape. Parasphenoid teeth in *A. oweni* are constant in shape and size throughout their extent. The vomer of both species bears a small, raised, transversely orientated tooth patch of small needle-like teeth. A specimen of *A. oweni* (B.M.N.H. 30528) shows this tooth patch to be partially subdivided into right and left halves (Woodward 1901 : pl. 4, fig. 2) suggesting the origin of the undivided condition in *A. vulpes* from paired elements.

The quadrate/mandibular articulation of *A. oweni* lies relatively further forward than in the type-species. The lower jaw is shorter, a feature accentuated by the relatively longer snout. A consequence of the greater suspensorial angle (Gregory 1933) is that the horizontal limb of the preoperculum is longer than the vertical limb. In *A. vulpes* the limbs are of equal length.

The differences mentioned above are minor and serve only to distinguish *A. oweni* as a distinct, but closely related species. To determine which is the more primitive is not easy. There are several differences which appear to have little or no significance in this case, such as the median frontal depression, deeper neurocranium and shorter jugular canal in *A. oweni*.

A. oweni appears more specialized than *A. vulpes* in having a relatively longer snout and a more forwardly positioned quadrate/mandibular articulation. In other features, however, there is a greater resemblance to the primitive *Osmeroides*, for example, the ornamentation, the ridge at the medial margin of the sub-epiotic fossa and the partially divided vomerine tooth patch.

The majority of specimens of *A. oweni* are isolated teeth or fragments of tooth plates, making specific determination difficult, particularly since the teeth associated with the crania described above are poorly preserved. However, if B.M.N.H. P.1697 (a group of teeth from the Lower Hamstead Beds of the Isle of Wight) is correctly identified, then this species must have extended to the Lower Oligocene (Lattorfian).

Albula eppsi White & Frost

1931 *Albula eppsi* White & Frost : 83–84, 105, figs. 137–14, pl. fig. 8.
1960 *Albula eppsi* White & Frost ; White : pl. 30, fig. 4.

DIAGNOSIS. See White & Frost 1931 : 83.

SYNTYPES. B.M.N.H. P.14628, P.14628a–b, tooth plates from the Blackheath Beds (Sparnacian), Abbey Wood, Kent, and P.15287 from the same horizon and locality.

MATERIAL. Twenty-three specimens in the B.M.N.H. consisting of fragmentary tooth plates and a small portion of an operculum.

HORIZON AND LOCALITY. Sparnacian–Cuisian, S.E. England.

REMARKS. White & Frost (1931) stated that the tooth plates referred to *A. eppsi* differ from those of the Recent species in showing teeth of equal size, with no diminution of tooth size towards the margin of the tooth plate. Such a regular tooth size is characteristic of the contemporaneous *A. oweni* and this fact probably motivated Casier (1966 : 134) to interpret *A. eppsi* as representing young individuals of *A. oweni*. However, the great difference in size between the two species and the total absence of intermediate forms suggests that this species is probably a valid one. *A. eppsi* is reminiscent of *Osmeroides latifrons* (Turonian) in being small and showing no diminution of tooth size towards the edge of the tooth plate.

Frost (in White & Frost 1931 : 105) referred an otolith to *A. eppsi*, presumably because it was found together with tooth plates of this species. This otolith is held by Frost to resemble those of *A. vulpes* in the rounded anterior and posterior rims.

Other albulid remains

There is in the B.M.N.H. collection a large series of isolated teeth from Tertiary deposits of Europe which, although albulid in form, are not easily referred to any of the species recognized so far. Until more associated material of various growth stages become available the specific identity of these teeth must remain in limbo.

Woodward (1901 : 73) referred to several specimens from the Gault Clay (Albian) which, he said, may be albulid. The specimens concerned (B.M.N.H. 47286, P.9159) are phyllodont tooth plates and should be referred to *Casierus* Estes or a closely related form.

In the B.M.N.H. collection there are two specimens, B.M.N.H. P.1224 and P.1225, which are albulid in form and come from the Upper Cretaceous of Red Deer River, Alberta, Canada. The specimens consist of isolated teeth and vertebrae. The teeth are unlike those of any *Albula* species in being laterally flattened and in showing a narrower base than crown. The vertebrae, which in lateral view are deeper than wide, are marked by numerous fine anastomosing strengthening bars.

There are records of other albulids from North America. Applegate (1970) has described a new species of *Albula*, *A. dunklei*, from the Mooreville Chalk (Santonian) of Alabama. Estes (1969c) erected a new monotypic albulid genus *Coriops amnicolus* for specimens from the Lance Formation of Wyoming and the Hell Creek Formation of Montana, the age of which, according to Cobban & Reeside (1962), is Maastrichtian–Danian. The albulid specimens found in Alberta, Wyoming and Montana are from freshwater deposits.

Other Upper Cretaceous albulids of N. America have been recognized on scale remains by Cockerell (1933), who described *A. antiqua* from Florida, and David (1940) who described a different genus, *Kleinpellia*.

Genus ***LEBONICHTHYS*** nov.

DIAGNOSIS. Albulid fish in which the frontals and pterotics show ornamentation in the form of weak ridges. Mouth terminal or nearly so. Maxilla extending to beneath the posterior half of the orbit, with or without teeth. Single elongate supramaxilla. Quadrate/mandibular articulation beneath posterior half of the orbit. Suboperculum large, equal in area to half that of the operculum. Gular plate large. Vertebral column with 64–66 vertebrae of which 23–24 are caudal. Centra deeper than long, marked laterally by 5–6 grooves. Anal fin situated nearer to caudal peduncle than to the pelvic fin.

TYPE SPECIES. *Osmeroides gracilis* Davis.

Lebonichthys gracilis (Davis)

(Text-figs. 88–91)

1887 *Osmeroides gracilis* Davis : 559, pl. 31, figs. 2, 3.
1887 *Osmeroides latus* Davis : 561, pl. 31, fig. 1.
? 1887 *Osmeroides brevis* Davis : 560, pl. 32, fig. 1.
1901 *Osmeroides gracilis* Davis ; Woodward : 16, pl. 2, figs. 1, 2.

DIAGNOSIS. *Lebonichthys* reaching 170 mm S.L. Head and opercular apparatus equal in length to 30 per cent of standard length. Parasphenoid with hemispherical teeth of irregular size. Ectopterygoid edentulous. Maxilla edentulous. Dorsal fin situated nearer to the occiput than to the caudal peduncle, with 24–25 rays. Caudal skeleton with three epurals, supporting neural spines unexpanded, fringing fulcra and caudal scutes present. Scales with anterior margin scalloped.

HOLOTYPE. Incomplete fish, R.S.M. 1891.59.86, from the Upper Santonian of Sahel Alma, Lebanon.

MATERIAL. The holotype and 16 specimens in B.M.N.H. All specimens are from the Upper Santonian of Sahel Alma, Lebanon.

DESCRIPTION. The head occupies 30 per cent of the standard length and is twice as long as it is deep. The anterior end of the snout is slightly truncated. The quadrate/mandibular articulation lies beneath the centre of the orbit. With the exception of the frontals and pterotics, the cranial bones are smooth.

Neurocranium. The neurocranium is shallow throughout. The roof is flat with the frontals forming the majority of its area. Each frontal meets its partner in a slightly wavy suture. Anteriorly the dermethmoid, which is smaller and simpler in shape than that of *Albula*, separates the frontals. The frontal tapers gradually toward the snout but there are two places where the frontal narrows sharply, at the level of the autosphenotic spine and again at the level of the lateral ethmoid. Posteriorly the frontal is indented where it meets the pterotic. The surface of the frontal is slightly raised at the centre of ossification. From this centre several ridges, with intervening grooves, curve anteriorly and laterally. The most medial of these ridges ends anteriorly in a foramen which marks the point of exit from the bone of the supraorbital sensory canal. Anterior to this level the canal continued in a shallow groove. The central portion of the skull roof exhibits a slightly depressed area. Faint ridges may also be seen passing posteriorly from the ossification centre of the frontal but these are weak compared to the anterior ridges.

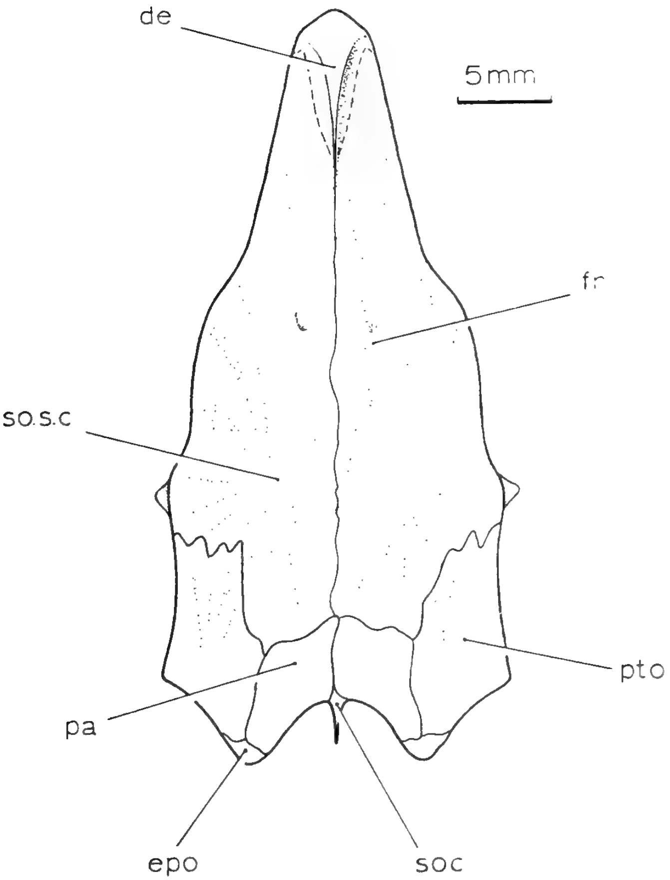

FIG. 88. *Lebonichthys gracilis* (Davis). Neurocranium in dorsal view. Based on R.S.M. 1891.59.85 and 1881.5.36.

The parietal is rhomboidal and meets its partner in a nearly straight median suture. Between them the parietals cover much of the supraoccipital and the epiotics, only the crest of the former and the processes of the latter being visible in dorsal view.

The pterotic meets the frontal in a syndesmotic union, the path of the suture line being due to the posterior margin of the frontal rather than the anterior border of the pterotic which lies beneath the frontal. The posterior margin of the pterotic is oblique and meets the lateral margin in a small laterally directed process which marks the posterior end of the hyomandibular facet. The surface of the pterotic is marked by fine ridges extending forwards from the centre of ossification. The otic sensory canal ran in a deep groove incompletely roofed by bone. Posteriorly the canal opened by a single pore at the level of the lateral prominence on the margin of the pterotic.

The anterior part of the neurocranium is defective in all specimens. The dermethmoid is incompletely known but a median vertical ridge may be seen in several examples. The nasal is a thin, gutter-shaped element partially overlapping the anterior end of the frontal.

Of the lateral neurocranial wall little can be seen. Features which may be recognized are a deep subtemporal fossa beneath the hyomandibular facet, a large otic bulla which accommodated the sacculith, and a very small autosphenotic spine. Imperfect suture lines between the various neurocranial elements are seen in some specimens. The outline and contours of those which may be identified suggest that the neurocranium is very much like that of *Osmeroides latifrons*. Significantly, the intercalar is reduced to a small cap of bone postero-ventral to the subtemporal fossa.

The parasphenoid is distinctive in bearing a dentition similar to that of small specimens of *Albula vulpes*. The bone is broad throughout its length. Posteriorly it reaches the occipital condyle, while anteriorly it overlies the vomer beneath the lateral ethmoid. At the level of the weakly defined ascending wings the parasphenoid exhibits a shallow angle. Posterior to this level the parasphenoid extends back and terminates in two short prongs, between which there is a median ventral groove extending forwards to the parasphenoid flexure. Beneath the orbit and part of the lateral ethmoid the parasphenoid bears a tooth plate. Each of the many teeth borne by this plate is hemispherical and bears a distinct translucent apical cap of enamel. There is a large pulp cavity. The posterior teeth are the smallest, the largest being found in the anterior third of the plate. Throughout the toothed area very small teeth may be seen lying adjacent to large ones. Towards the lateral margin of the plate there is a predominance of smaller teeth. The base of the ascending wing of the parasphenoid is marked by a deep excavation at the bottom of which lies the foramen for the internal carotid artery. The efferent pseudobranchial artery must have looped around the antero-dorsal margin of the parasphenoid ascending wing.

The vomer is as wide as the anterior end of the parasphenoid, with which it is in contact in an overlapping suture. No specimen shows definite evidence of vomerine teeth although several small needle-like teeth, which may probably be referred to the vomer, are often found in the snout region.

Hyopalatine bones. The hyomandibular is stout and relatively short. Dorsally the bone is thick and forms a single broad articular head. The bone projects anteriorly as a thin wing which meets the metapterygoid. Characteristically, there is little or no overlap between these elements. The ventral part of the hyomandibular slopes forwards as a stout shaft, the posterior margin of which is grooved for the passage of the hyomandibular trunk of VII and the efferent hyoidean artery. The opercular process is weakly defined.

The metapterygoid is of irregular shape. Anteriorly this element overlaps the endopterygoid while ventrally it is separated from the quadrate by a narrow interspace. The postero-ventral margin of the metapterygoid overlaps the symplectic, as in other albuloids.

The symplectic is long in *Lebonichthys* and provides a firm linkage between the forwardly positioned quadrate and the ventral end of the hyomandibular. Posteriorly the symplectic is somewhat flattened.

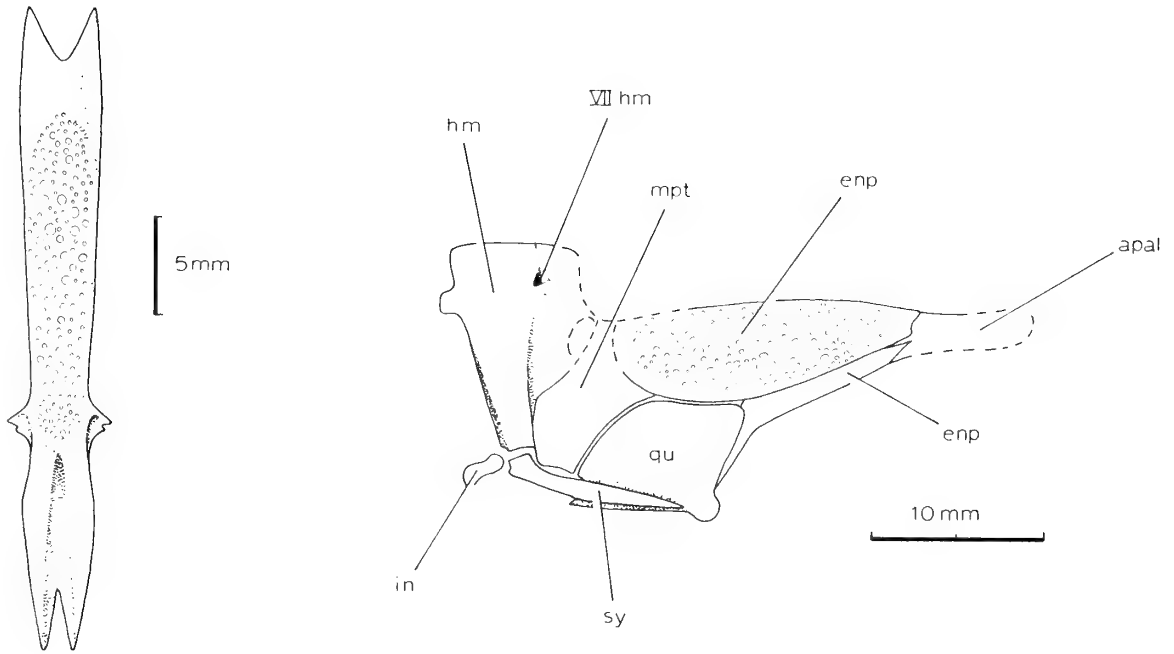

FIG. 89. *Lebonichthys gracilis* (Davis). Left: parasphenoid in ventral view. Right: hyopalatine bones of left side in medial view. Composites of several B.M.N.H. specimens.

The quadrate is fan-shaped. The posterior or ventral margin lies almost horizontally, with the expanded condyle directed antero-ventrally. A groove on the medial surface of the quadrate received the lower end of the symplectic.

The postero-ventrally inclined limb of the ectopterygoid fits tightly around the anterior border of the quadrate. The longer antero-dorsally inclined limb runs along the entire length of the endopterygoid. A shallow crest of bone arises from the dorsal margin of the ectopterygoid at the angle in the bone. This crest is similar to that developed in *Osmeroides latifrons* and homologous with the peculiarly shaped ectopterygoid process of Recent albuloids. The endopterygoid is oval, at least three times as long as wide. The convex buccal surface bears a large patch of teeth of the same form but of smaller average size than those borne by the parasphenoid. The anterior limit of both endopterygoid and ectopterygoid is difficult to decipher in any specimen as this region is covered by the crushed remains of a spongy ossification representing a weakly ossified autopalatine. The autopalatine of Recent albulids is only weakly ossified in large individuals. The anterior end of the autopalatine in *Lebonichthys* is represented by a rounded knob formed of more compact bone than that posteriorly. The palatine head articulates with the mesethmoid medially and the inner face of the maxillary head anteriorly. B.M.N.H. P.4855 shows a small patch of palatine teeth which are villiform in shape, not needle-like as in *Albula*.

Dermal upper jaw. Those specimens exhibiting a premaxilla indicate that there was a very close union between this element and the ethmoid. The premaxilla is broad anteriorly where it meets its partner in the mid-line. Posteriorly the alveolar portion is tapered. The lateral surface of the premaxilla is marked by two or three pores but interconnecting canals cannot be traced ; thus the presence of a premaxillary sensory canal is known by inference rather than from direct evidence. A narrow band of fine, needle-like premaxillary teeth is found along the slightly convex oral border.

Unlike the premaxilla, the maxilla is often found dissociated from the neurocranium. Anteriorly the expanded head of the maxilla turns dorsally and medially. Posteriorly the maxilla expands into a shallow ovoid which is overlain postero-dorsally by a single elongate supramaxilla. The maxilla is grooved dorsally behind the maxillary head and ventrally beneath the head. The dorsal groove marks the position occupied by the overlying first infraorbital. The ventral groove contained the alveolar portion of the premaxilla. The maxilla is edentulous.

Mandible. The mandible is short and bears a prominent coronoid process developed towards the posterior end of the jaw. The dentary symphysis is turned slightly ventrally. Distinctive albuloid features of the mandible are the inflected ventral margin and the presence of a deep groove containing the mandibular sensory canal. The mandibular sensory canal was not covered by bone ventrally. The dentary bears a band of needle-like teeth along the oral margin. Posteriorly the articular forms the articulatory cup. The medial surface of the mandible bears a large endosteal articular and sesamoid bone.

Hyoid arch, branchiostegal rays, gular plate and gill arches. The ceratohyal is, as usual in teleosts, ossified in two sections, a large anterior and small posterior element. The former is represented by a thick bone which is constricted in the anterior third.

The anterior end is shallower than the posterior end. The posterior ceratohyal is thinner than the anterior element. The ventral margin of the posterior ceratohyal is curved while the dorsal margin is straight, except posteriorly where the border is notched for the reception of the interhyal. Both dorsal and ventral hypohyals may be identified but little of their shape may be seen. Each hypohyal consists of a core of spongy bone covered by a thin perichondral shell. The anterior tip of the hypohyals lies between and level with the lower jaw articulation when the mouth is closed. The dorsal edge of the anterior ceratohyal is grooved for the afferent hyoidean artery. The depth of this groove is comparable with that seen in *Albula.*

There are 12–14 branchiostegal rays. The first (or most posteriorly situated) branchiostegal is broad and supported solely by the posterior ceratohyal. The second of the series articulates with the hyoid bar at the junction of the two ceratohyals. The branchiostegals become progressively thinner at the anterior end of the series. Anteriorly, the last ray in the series may have lain free in the branchiostegal membrane since it is often displaced and shows no development of an articulatory head.

A large gular plate is attached to the posterior edge of the dentary symphysis. The width of this plate, equivalent to over one-third of the mandibular length, suggests that the lower jaw rami were wide apart. It is significant that in many specimens the jaw rami are often seen splayed apart. The size of the gular plate would preclude any interpretation of the gular lying vertically as it does in the Recent *Albula.*

The basibranchial and basihyal elements are poorly known. A large basibranchial tooth plate lies in a position (with respect to the hypobranchials) suggesting that it represents the fusion of the first three basibranchial plates. The dorsal surface of this plate bears many villiform teeth. The posterior end of a basihyal tooth plate is seen in B.M.N.H. P.4764. The plate appears edentulous.

The hypobranchials of the first three arches are developed in typical fashion. The first is the longest of the series and shows a slight curvature. The second, like the first, shows a distinct basal articulatory head proximally, but the short third hypobranchial appears merely as an ' outpushing ' from the third basibranchial. The five ceratobranchials are typical in that the first is substantially longer and broader than the fifth. The latter elements share a small mutual interface. Small, irregular tooth plates, each with many needle-like teeth, are associated with the oral surfaces of the ceratobranchials. These tooth plates are relatively sparse : for instance six are detectable upon the fourth ceratobranchial of B.M.N.H. P.4764. A single large tooth plate is associated with the medial margin of the fifth ceratobranchial. This tooth plate, the lower pharyngeal, has the shape of an isosceles triangle, twice as tall as wide with the apex directed anteriorly.

Well-defined gill-rakers were not seen on any but the first ceratobranchial. The gill-rakers have the same form as those of *Albula* and *Pterothrissus.* Nothing of the dorsal gill arch elements was seen.

Circumorbital bones. The supraorbital was not positively identified in any specimen but several exhibit small splinters of bone indicating that its form was as in Recent albuloids.

Similarly, the infraorbitals are incompletely known. The orbital margin of this series is gently rounded, as in *Albula* but in contrast to *Pterothrissus*. Anteriorly, the dorsal margin of the first infraorbital is straight and inclined towards the snout tip. The first infraorbital overlaps the dorsal half of the maxilla. The posterior members of the series cover the cheek region posteriorly to the level of the hyomandibular. The orbital margin of the infraorbitals is rolled over laterally to provide a partial protection for the infraorbital sensory canal.

Opercular series. The operculum is as wide as it is deep. Its anterior and dorsal margins are straight. The posterior margin passes ventrally and slightly posteriorly before turning sharply to present an almost horizontal ventral margin. The operculum forms a comparatively small part of the entire cheek region.

The suboperculum is a large element as in all albuloids. The posterior and ventral margin is smoothly rounded and continues the contour of the operculum. Anteriorly the suboperculum sends up a small dorsal wing. The shape of the interoperculum could not be determined.

The preoperculum is incompletely known. The anterior margin lies tightly against the hyomandibular, symplectic and quadrate. A deep groove, which is partially overlain by bone, runs close to the anterior margin and represents the path taken by the preopercular sensory canal.

Pectoral girdle and fin. Dorsally the pectoral girdle is attached to the neurocranium by the small post-temporal. Three limbs are directed anteriorly from the main body of the post-temporal which is represented by a small triangular plate. One such projection (the dorsal limb) reaches above the epiotic to which it was no doubt connected by ligaments. Another is short, laterally directed and lies in juxtaposition to the postero-lateral corner of the pterotic and is homologous with a similar limb seen in *Albula*. The third limb (the ventral limb) passes antero-ventrally to contact the neurocranium in the region of the intercalar.

The supracleithrum overlaps the cleithrum ventrally and is itself overlain dorsally by the post-temporal. The supracleithrum is longer than broad, with its anterior and posterior margins parallel. From its union with the post-temporal the bone slopes postero-ventrally.

The cleithrum is, as usual, the largest element of the girdle. As seen in lateral view the bone is tapered both dorsally and ventrally. The posterior margin slopes ventrally at a steep angle and in this respect resembles *Pterothrissus*. The endochondral elements are too incompletely known to warrant comment. However, in lateral view the posterior limit of these elements lies behind that of the overlying cleithrum, as in all albuloids.

There are at least 12 pectoral fin-rays (Davis 1887 quotes a figure of 14 for all species here considered as *Lebonichthys*). The first ray is unbranched. The dichotomy of the inner rays is confined to the distal third of their length. A small triangular splint is associated with the base of the outer fin-ray.

Pelvic girdle and fin. The only evidence of the pelvic girdle is a small, transversely orientated strip of spongy bone immediately anterior to the bases of the fin-rays. The anterior half of the pelvic girdle, if present, was probably represented by cartilage.

The pelvic fin originates beneath the posterior half of the dorsal fin. The pelvic fin is made up of 9–10 rays, the outermost being both the longest and the only unbranched member of the series. Associated with the base of the upper half of the outer ray there is a large pelvic splint bone. The anterior end of this splint is curved dorsally and lies free from the fin-ray bases.

Vertebral column. One specimen, B.M.N.H. P.9162, is sufficiently well preserved for a vertebral count to be made. This specimen has a total of 66 preural vertebrae of which approximately 23 are caudal.

Each centrum is deeper than long. Those of the anterior abdominal region are considerably deeper relative to their length than those of the caudal region. The centra are marked laterally by four to six longitudinal grooves separated by ridges.

The neural arches are autogenous throughout the column. In the anterior abdominal region the neural arches are expanded distally but in the posterior abdominal and caudal region such expansions are not seen. The neural spines of the anterior abdominal region are fine, straight and the paired halves remain separate. Posteriorly the spines of either side are fused to form a median structure which exhibits a slight backward curvature. The posterior neural spines are somewhat modified to support the caudal fin-rays.

The parapophyses are autogenous. Throughout most of the abdominal region they are represented by small knobs lodged in cup-shaped depressions in the anterior half of the centra. The posterior five or six parapophyses are somewhat longer, the last being the longest and bearing a correspondingly shorter pleural rib.

Each pleural rib is fine, slightly curved and incompletely encircles the abdominal cavity, substantiating the view that this fish had a rounded body. Except posteriorly, where the ribs are borne solely by the lengthened parapophyses, the articulation of the ribs is shared between the parapophysis and the centrum.

The haemal arches are inserted into depressions in the centra. Distally the arches bear slightly curved haemal spines. The posterior five are modified to support the caudal rays.

There are 11–12 supraneurals associated with the first 17–18 neural spines. Each supraneural is sigmoid in shape and they form a graded series from large and broad anteriorly to small and narrow posteriorly.

Epineurals are found throughout the column. Anteriorly they are attached to the posterior margin of the neural arch/spine junction. In the posterior part of the column they are often displaced and in life probably lay free in the myocommata.

Epipleurals are also present throughout the column. In the abdominal region they were closely applied to the parapophyses but throughout the caudal region they lay free. The epipleurals in the anterior caudal region show forked bases.

Median fins. The dorsal fin is relatively long based, the base length being equal to 28 per cent of the standard length. The origin of the fin lies near the occiput and the occiput–origin distance is considerably less than the distance from the termination of the fin to the caudal peduncle, a feature previously noted by Woodward (1901 : 16).

The dorsal fin is composed of 24–25 rays. Davis (1887 : 560, pl. 31, fig. 2) states that there are 32 rays but his illustration does not support such a high count. Woodward

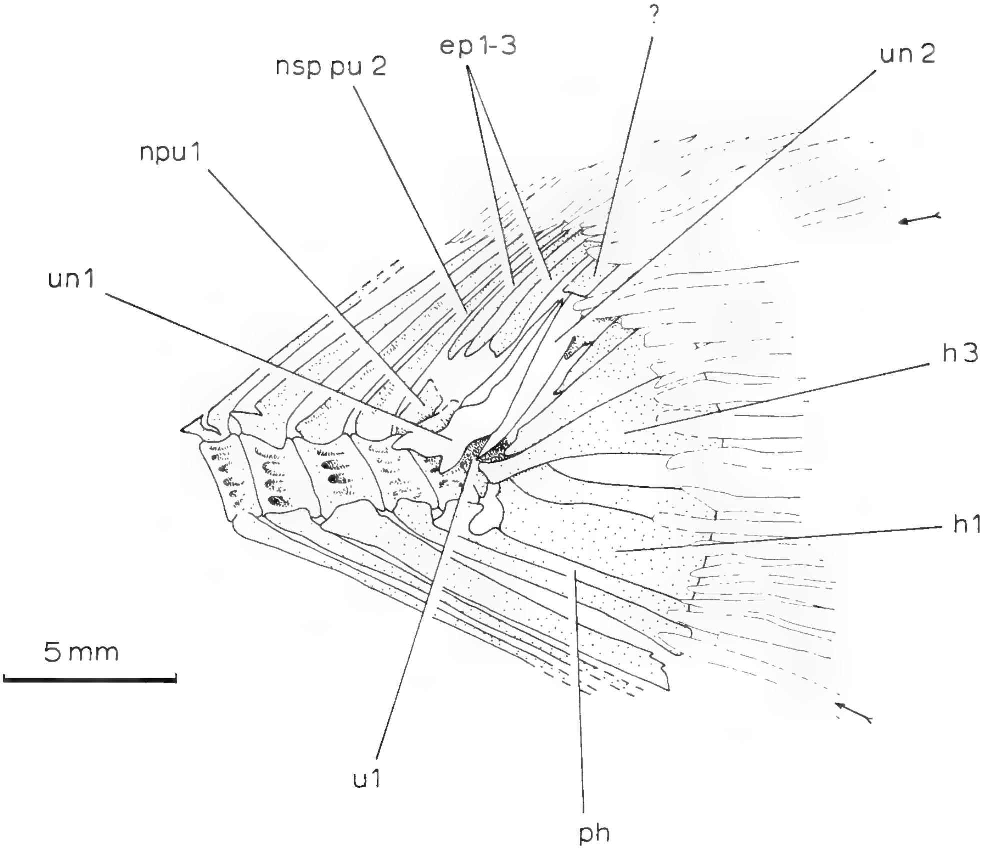

FIG. 90. *Lebonichthys gracilis* (Davis). Caudal skeleton in left lateral view. Arrows indicate upper and lower principal fin-rays. Camera lucida drawing of B.M.N.H. P.4856.

(1901 : 16) quotes a figure of 20. The first two rays are unsegmented. The fifth ray is both the longest and the first branched. Of the 21 pterygiophores the first three support the first six fin-rays. With the exception of the first three, each pterygiophore consists of three distinct radial ossifications. The exceptional pterygiophores exhibit fusion between the proximal and middle radials.

The anal fin arises nearer to the caudal peduncle than to the pelvic fin and consists of nine rays supported on seven pterygiophores. The anterior two rays are unsegmented and the fourth is both the longest and the first branched.

The caudal fin-rays are supported by five preural and two ural centra. Each of the preural centra is deeper than long and marked by ridges. The ural centra are smooth and largely overlapped by the uroneurals and the hypural heads. In the specimen figured (Text-fig. 90) the second ural centrum is completely obscured by the uroneurals.

The haemal spines of the five preural vertebrae become progressively stouter from the fifth to the first (the parhypural). The parhypural shows the characteristic notch in the posterior margin. This notch lies in juxtaposition to a notch in the anterior margin of the first hypural and marks the divergence of two lateral caudal arteries from the median dorsal aorta.

Dorsally, the neural spines associated with the second to fifth preural centra are slender, each with a stout posterior edge preceded by a thin median wing. The tips of the last three neural spines converge to support the anterior dorsal accessory rays. The neural arch complex associated with the first preural centrum appears to be a double structure, i.e. two neural arches set one behind the other. This arrangement is open to three interpretations. It may represent the two lateral halves of a single first preural neural arch, these having become displaced relative to one another during preservation (in this connection it is interesting to note that in one specimen of *Pterothrissus* examined the two halves of this arch remain distinct from one another except at their extreme tips). Secondly, it may represent a double neural arch upon this centrum ; such a condition is quite common in lower teleosts and has been recorded for *Tarpon* (Hollister 1936 : fig. 16). The third interpretation is that the posterior structure is the neural arch of the first ural centrum which has become displaced anteriorly (cf. Nybelin 1971). Examination of other specimens failed to substantiate any of these interpretations.

There are at least two uroneurals. The first is large and shows a forked base overlapping the first and part of the second preural centrum. The second uroneural is long, extending from a lateral overlap of the first ural centrum to well beyond the distal extremity of the first uroneural (a typical albuloid disposition). Specimen B.M.N.H. P.4856 shows a small element which overlaps the dorsal extremity of the second uroneural. Its appearance suggests a uroneural, yet the bone, which shows no sign of having been broken, is truncated, unlike a uroneural. Distally this element reaches between the bases of the posterior dorsal basal fulcra.

The first and second hypurals are supported by the first ural centrum. Distally the hypurals support the principal fin-rays of the lower caudal lobe. As is usual among lower ' isospondyls ' the first hypural is the larger and has a characteristically narrow articular head. In the specimen figured the lower hypurals have been slightly displaced postero-ventrally from their true position.

Four upper hypurals support the principal rays of the upper lobe. The third hypural is large and is the only member of the upper series showing a distinct articulatory head. The uppermost hypural is very small and may represent a fusion of two elements since there is a faint line of division running down the length of this hypural. In the specimen figured the upper hypurals have been displaced antero-ventrally.

Between the first uroneural and the last neural spine there are three epurals, the distal extremities of which are obscured by the bases of the basal fulcra which they support.

There are 19 principal rays, 10 in the upper lobe and 9 in the lower. The uppermost principal ray is large, unbranched and does not extend over any endochondral element (cf. Patterson 1968a). The innermost principal rays do not show expanded bases and are thus similar to those of Recent albuloids. The lowermost principal ray is supported by the parhypural and the second preural haemal spine.

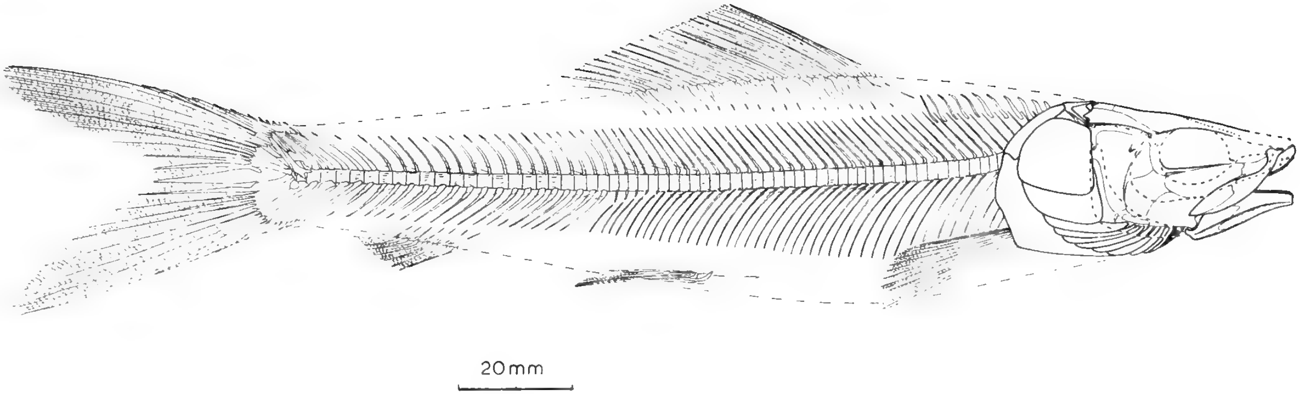

FIG. 91. *Lebonichthys gracilis* (Davis). Entire skeleton, scales omitted.

There are 10–11 dorsal basal fulcra succeeded by three or four fringing fulcra. The posterior five basal fulcra show articulations. Seven basal fulcra occur ventrally and are supported by the haemal spines of the third to fifth preural centra.

An elongate caudal scute occurs above and below the caudal peduncle.

Squamation. The scales are cycloid. The posterior margin of the scale is rounded, the anterior margin straight. Concentrically arranged circuli are apparent in the anterior and lateral fields, while the posterior field is marked by a few granulations. Anteriorly there are five to eight radii which produce a scalloped anterior margin.

Lebonichthys lewisi (Davis)

(Text-fig. 92)

1887 *Clupea lewisii* Davis : 571, pl. 33, fig. 1.
1901 *Osmeroides lewisi* (Davis) Woodward : 17, pl. 2, fig. 3.

DIAGNOSIS. *Lebonichthys* reaching 260 mm S.L. Head equal to 30 per cent S.L. Vomer with villiform teeth. Maxilla with small villiform teeth. Dorsal fin situated nearer to the caudal peduncle than to the occiput, and composed of 18–19 rays. Caudal skeleton with two epurals ; the supporting neural spines expanded anteroposteriorly ; fringing fulcra absent. Caudal scutes present. Scales without scalloped margin.

HOLOTYPE. Nearly complete fish, R.S.M. 1891.59.91, from the Middle Cenomanian of Hakel, Lebanon. The counterpart is B.M.N.H. P.4868.

MATERIAL. The holotype, counterpart and B.M.N.H. P.6024 from the Middle Cenomanian of Hakel, Lebanon.

REMARKS. *Lebonichthys lewisi* is known by only two individuals of which one, the holotype (part and counterpart), is poorly preserved. Little information on the head is available from these specimens.

Known features of the cranial roof closely resemble those of *Lebonichthys gracilis* and *Osmeroides latifrons*. The frontals are wide above the otic and orbital regions but taper above the slightly elongated snout. A long tubular nasal is present. The lateral ethmoid is a large, stout ossification, more robust than that of *L. gracilis* but like that of *Albula*. There is no direct contact between the lateral ethmoid and parasphenoid as there is in *Albula*.

The parasphenoid attains its greatest width beneath the lateral ethmoid, as in *O. latifrons*. Teeth are borne on the ventral surface of the parasphenoid beneath the orbit. The parasphenoid teeth are all of the same size but their shape varies from conical to hemispherical. The vomerine teeth are villiform ; the limits of the supporting ossification are not known.

The hyopalatine series is similar to that of *L. gracilis* except for two obvious differences : the metapterygoid only contacts the symplectic over a short area and there are teeth on the ectopterygoid in addition to those on the endopterygoid. The presence of ectopterygoid teeth is a primitive feature, known only in *L. lewisi* among

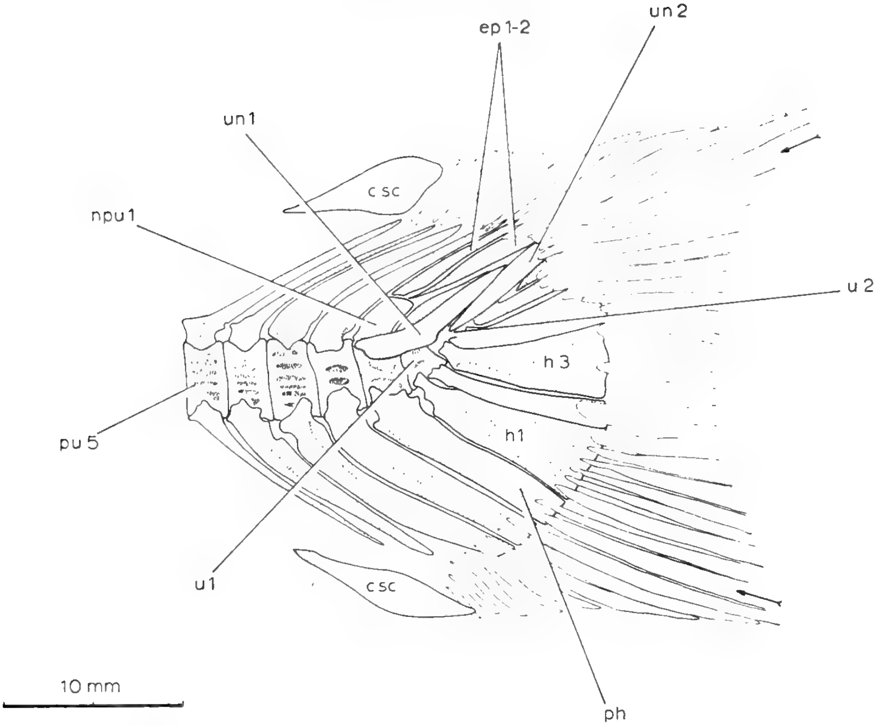

FIG. 92. *Lebonichthys lewisi* (Davis). Caudal skeleton in left lateral view. Arrows indicate upper and lower principal fin-rays. Camera lucida drawing of B.M.N.H. P.6024.

albulids. Ectopterygoid teeth of *L. lewisi* resemble those of *O. latifrons.* The teeth on the dermopalatine are villiform, as in *L. gracilis.*

The upper jaw extends to the level of the middle of the orbit in B.M.N.H. P.6024 and to the posterior margin of the orbit in P.4868. The curvature of the oral surface is not as marked as in *L. gracilis.* The teeth on the premaxilla and maxilla are villiform in P.6024, more pointed in P.4868, but never needle-like as in *L. gracilis.*

The mandible extends from the snout to beneath the middle of the orbit in P.6024. It is slightly longer in P.4868. The dentary teeth are set in a band along the oral surface and resemble those of the upper jaw ; villiform in P.6024 and pointed in P.4868.

The operculum is slightly deeper than wide with an oblique ventral margin, thus contrasting with that element in *L. gracilis.* In shape the preoperculum resembles that of *Osmeroides.* The sensory canal appears to have been completely enclosed by bone.

There are at least 15 branchiostegal rays borne by the ceratohyals. When the mouth was closed the anterior end of the hyoid bar must have lain between the jaw rami. The gular plate is narrower than in *L. gracilis.*

The pectoral girdle is not known to differ much from that of *L. gracilis.* The post-temporal of *L. lewisi* has the dorsal and ventral limbs but a central limb is absent.

The cleithrum is large, much of its area being given over to muscle attachment. There are at least 10 pectoral fin-rays. The pelvic fin shows 11 rays.

The vertebral column is composed of approximately 64 vertebrae, of which 24 are caudal. Over most of the column the neural arches and spines, haemal arches and spines and the parapophyses and ribs are precisely the same as in *L. gracilis*. Differences occur in those preural vertebrae associated with the caudal fin-rays. Epineural and epipleural (ventral) intermusculars are present throughout the column. There are 22–23 supraneurals, more than in *L. gracilis*, and this reflects a difference in the position of the dorsal fin which in *L. lewisi* is situated nearer to the caudal peduncle than to the occiput. The dorsal fin contains 18 or 19 rays. B.M.N.H. P.4868 shows 10 anal pterygiophores indicating that the anal fin was composed of approximately 12 fin-rays; B.M.N.H. P.6024, however, has 7 pterygiophores and 9 rays.

The caudal skeleton of *L. lewisi* (Text-fig. 92) is more like that of *Albula* than is that of *L. gracilis*. In *L. lewisi* the supporting neural and haemal spines are expanded antero-posteriorly, there are two epurals and both uroneurals are stout and disposed in typical albuloid fashion. The proximal end of the first uroneural is expanded. This is similar to *L. gracilis* but unlike *Albula vulpes*. As is usual in albulids, the neural spine on the second preural centrum is full length.

What is known about the skull of *L. lewisi* suggests that it is more primitive than that of *L. gracilis*. The jaws are relatively longer and less specialized, and the dentition borne by the dermal jaws, palate and basibranchial elements is also more primitive. The caudal skeleton, however, appears more specialized than that of *L. gracilis*, approaching the *Albula* condition.

IV. DISCUSSION OF THE ORDER ELOPIFORMES

(a) *Historical*

With the exception of the pterothrissids, the fishes grouped here as the order Elopiformes have been referred to the families Elopidae and Albulidae by Woodward (1901), Boulenger (1910), Barnard (1925) and Fowler (1936). *Pterothrissus* (*Bathythrissa*), on which the family Pterothrissidae is based, has been associated with the Salmonidae by Gunther (1877), and the Clupeidae by Gill (1893). A suggestion by Boulenger that *Pterothrissus* is closely related to *Albula* was confirmed by Ridewood (1904) who placed the genus in the Albulidae. This author also endorsed Woodward's view (1901) that the Cretaceous *Istieus* is closely related to *Pterothrissus*. Since that time *Istieus* and *Pterothrissus* have been considered as constituting a separate family, closely related to the Albulidae (Berg 1940) or as a subfamily of the Albulidae (Norman 1960) or as members of the family Albulidae (Boulenger 1910).

The fishes grouped in the Elopidae by Woodward (1901) and others have often been divided into two families, the Elopidae and the Megalopidae, which in turn were grouped as a higher taxon of equal rank with that containing the Albulidae and Pterothrissidae (Berg 1940; Jordan 1923). Little indication, other than text order, was given as to the relationship existing between the Elopidae (+ Megalopidae) and the Albulidae (+ Pterothrissidae) or to their relationship with other ' clupeiform ' fishes.

Bertin and Arambourg (1958) went one stage further by including the Elopidae (containing the megalopids), Albulidae and Pterothrissidae in a suborder Elopoidei of the order Clupeiformes (*sensu lato*). In the Elopoidei Bertin and Arambourg (*op. cit.*) also included the extinct family Thrissopateridae (*Thrissopater* and *Pachyrhizodus*), an assemblage thought by the present author to be but distantly related to the elopiforms.

Although the elopids, megalopids, albulids and pterothrissids have been considered closely interrelated by the above authors, the reasons put forward are based upon the common possession of primitive and retentional features. Characters often quoted as indicating relationship are: medially united parietals, gular plate, upper jaw formed by both the premaxilla and maxilla, posterior circumorbitals large, opercular apparatus complete, scapular foramen entirely enclosed, etc. Ridewood (1904 : 54) recognized the fallacy of using such criteria when he stated ' Such resemblances as exist between them [albulids and elopids] are explicable by the fact that neither has departed to any great extent from the ancestral group from which all the Teleostean fishes sprang . . . '. It is indeed true that none of the elopiform fishes has progressed far beyond the pholidophorid stage. *Elops* is justifiably credited with being the most archaic of living teleosteans and some authors have gone so far as to suggest that *Elops* is a holostean. Saint-Seine (1949), for instance, places *Elops* in the Halecostomi and Nybelin (1956) suggested that *Elops* is as much a holostean as is *Amia* or *Lepisosteus*. Gosline (1971 : 112, fig. 28) questions a close relationship between *Elops* and *Albula*, and implies that elopoids and albuloids may each have closer relatives outside the Elopiformes.

Clearly a relationship, if it exists, between the Elopidae, Megalopidae and the Albulidae and Pterothrissidae, must be based upon advanced and specialized characters inherited from the common ancestor. The presence of rostral ossicles and a leptocephalus larva, both considered here to be advanced features, were recognized by Bigelow (1963) as evidence of relationship, and this view is supported here.

The classification of the Elopiformes I have used is essentially that of Greenwood *et al.* (1966) with the addition of a new family, the Osmeroididae, to the Albuloidei. I believe that this scheme most closely reflects the phylogeny of the elopiform fishes.

The history of thought concerning the relationship of the elopiforms to other ' lower teleosts ' has been stable. Most authors have placed the elopiform families near to the clupeids with the implication that the latter are their closest living relatives (Boulenger 1910; Berg 1940; Bertin & Arambourg 1958; and others). Woodward (1901), perhaps significantly, dealt with the osteoglossids and notopterids between the elopiforms and clupeids.

Greenwood *et al.* (1966) consolidated a strengthening opinion that the ' isospondyls ' represent an artificial assemblage and proposed a three- or fourfold origin of teleosts from pholidophorid ancestors. In this scheme the elopiforms were considered to have evolved from the pholidophorids independently of other lower teleostean fishes with the possible exception of the Clupeiformes (Clupeidae, Engraulidae, Chirocentridae and Denticipitidae). Subsequent work has indicated that the clupeiforms possibly represent yet another attainment of the teleostean grade (Greenwood 1970b). The nearest relatives of the Elopiformes were thought by Greenwood *et al.* (1966) to be the Anguilliformes and the Notacanthiformes. Together these orders were grouped in a Division I (subsequently named Cohort Taeniopaedia by Greenwood, Myers, Rosen & Wietzman 1967) by virtue of the fact that members of all three orders have a leptocephalus larva, and certain other characteristics (Greenwood *et al.* 1966) ; the Elopiformes share the presence of rostral ossicles with the Notacanthiformes, and the Notacanthiformes are related to the Anguilliformes by a similarity in swimbladder anatomy.

(b) *Salient features of the Elopiformes and the relationship with other ' lower teleosts '*

The following list of salient characters has been drawn up to serve three main purposes : to indicate the wealth of primitive characters shown by the elopiforms ; to serve as a reference point by which comparisons with other teleosts may be made ; and to supplement the diagnosis given on p. 6.

1. Parietals in contact medially.
2. Dermethmoid separate from underlying mesethmoid.
3. Supraoccipital small, supraoccipital crest weakly developed.
4. Nasals slender, laterally placed.
5. Neurocranium well ossified in the otic region.
6. Post-temporal fossa with roof.
7. Subtemporal fossa large.
8. Orbitosphenoid and basisphenoid well developed.
9. Parasphenoid with teeth.
10. Anterior myodome bone absent.
11. Pars jugularis long ; separate lateral openings for the hyomandibular ramus of VII, jugular vein and orbital artery.
12. Hyomandibular broad, orientated vertically or nearly so.
13. Palatine composed of separate autopalatine (or palatine cartilage) and dermopalatine.
14. Premaxilla and maxilla entering gape. Supramaxilla(e) present.
15. Endochondral elements of the gill arches ossified, remaining separate from the dermal elements.
16. Basibranchial (and usually a basihyal) tooth plate well developed.
17. Ceratohyal composed of anterior and posterior ossifications, separated by a narrow band of cartilage.
18. Two hypohyals.
19. Urohyal shallow.
20. Infraorbital series composed of six elements. The first is large and is followed by a narrow second element.
21. Antorbital with associated sensory canal.
22. Infraorbital sensory canal branches anteriorly to form an antorbital branch and an ' ethmoid ' branch.

23. Opercular apparatus complete, with a large suboperculum and large interoperculum.
24. Pectoral girdle with a mesocoracoid arch articulating ventrally with both the scapula and coracoid.
25. Coracoid large.
26. Pectoral fin held low down on the body.
27. Pelvic fin abdominal, held horizontally, with more than 10 rays.
28. Pelvic splint bone present.
29. Vertebral centra pierced for the passage of the notochord. Neural arches, haemal arches and parapophyses autogenous.
30. Neural spines in the anterior abdominal region composed of separate lateral halves.
31. Supraneurals forming a complete series between the occiput and the origin of the dorsal fin.
32. Epineural intermuscular bones developed throughout the column.
33. Caudal fin forked.
34. Caudal skeleton with two free ural centra, uroneurals free from centra, hypurals separate from one another and from the ural centra. Parhypural without a hypurapophysis.
35. Nineteen principal caudal fin-rays ; 10 in the upper lobe, 9 in the lower.
36. Scales cycloid, with bone cells.
37. Lateral line complete.
38. Swimbladder with anterior outpushings developed on either side of the midline.
39. Retroarticular absent.
40. Development of a leptocephalus larva.
41. Rostral ossicles present.
42. Pectoral splint present at the base of the outermost fin-ray.
43. Basipterygoid process absent.
44. Mesethmoid weakly ossified or absent.
45. Ectopterygoid process present (its development varies within the order).
46. Supraorbital and infraorbital canals connected above the sixth infraorbital.

In addition, there are many other primitive characters found in the basal family (the Elopidae) of the order. These are listed below :

47. Body fusiform, showing little compression, fins acuminate.
48. Cranium shallow, mouth terminal.
49. Neurocranium shallow, skull roof flat.
50. Cephalic sensory canals enclosed by bone.
51. Supraorbital sensory canal extending to the parietal.
52. Dilatator fossa with roof.
53. Ethmoid commissure complete, contained within a bony tube that runs across the dermethmoid.
54. Intercalar large, and with the prootic forming an intercalar-prootic bridge.

55. Occipital condyle formed by the exoccipitals and basioccipital. Together these elements articulate with a vertebral centrum which is functionally part of the neurocranium.
56. Vomer short, with a broad head which bears a paired patch of small teeth.
57. Anterior ceratohyal with an elongate tooth patch plastered along the dorsal margin.
58. Branchiostegal rays numerous.
59. Gular plate large, horizontal.
60. Premaxilla small, forming little of the functional upper jaw.
61. Gill arches with suprapharyngobranchials associated with the first and second epibranchials. A fifth epibranchial is present.
62. Mandible with low coronoid process situated posteriorly.
63. Posterior infraorbitals broad, covering much of the cheek.
64. Dermosphenotic (sixth infraorbital) large.
65. Supratemporals large, meeting one another in the mid-line with the consequence that the supratemporal commissure is wholly enclosed by bone.
66. Anterior uroneural with forked base.
67. Seven hypurals.
68. Base of the innermost principal fin-ray of each caudal lobe expanded and considerably overlapping the supporting hypural.
69. Urodermal present.
70. Fringing fulcra usually present (but absent in *Elops*).

Of the characters listed above, 1–39 and 47–70 are primitive for teleosts,[1] the majority being found in the less specialized representatives of the superorders Clupeomorpha, Osteoglossomorpha, Protacanthopterygii (*sensu* Rosen & Patterson 1969) and Ostariophysi. These characters are therefore of little use in indicating relationships; they merely serve to suggest ways in which the elopiforms have not evolved. No other group of ' lower ' teleosts shows such a wealth of primitive characters and it is clear that the Elopiformes could not have evolved from any extant member(s) of the superorders mentioned above. Indeed, as noted below, it is extremely unlikely that elopiforms evolved from any known fossil teleost group belonging to the other superorders.

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[1] Feature 38, the possession of anterior diverticula of the swimbladder is included here as a character which is primitive for teleosts. The evidence is admittedly indirect, since there are no details of swimbladder anatomy in fossils except where that organ influences osteological development. Within the 'lower' teleosts an otophysic connection involving an anterior diverticulum of the swimbladder extending forward to the level of the neurocranium has developed in the Megalopidae (Elopomorpha), the Clupeomorpha, and in the Notopteroidei and the young growth stages of Mormyriformes (both Osteoglossomorpha). The development of otophysic connections in these groups, which are presumed to have evolved in parallel (Greenwood *et al.* 1966), suggests that some rudimentary swimbladder modification was present in the Pholidophoridae. The stage hypothesized for the pholidophorid condition may be seen in *Albula*, where paired anterior diverticula extend forward to terminate beneath the ventrolateral surfaces of the basioccipital (Greenwood 1970a); such diverticula are present, although poorly developed, in *Elops* and *Pterothrissus*. It is of interest to note that ostariophysan fishes, which are thought to have evolved from a group (the Salmoniformes, see Greenwood *et al.* 1966) without anterior diverticula of the swimbladder, developed an otophysic connection by vertebral and rib specializations (Rosen & Greenwood, 1970).

Features 43–46 are advanced to some degree over the basic teleost condition but may be seen in a large number of distantly related teleosts and have probably arisen independently in a number of lineages. They are therefore of limited use in indicating relationship.

Only three characters (nos. 40, 41 and 42[2]) indicate that the Elopiformes represent an interrelated assemblage of fishes distinct from other ' lower ' teleosts. Elopiforms show the specialized character combination of a leptocephalus, rostral ossicles and pectoral splint bone. The leptocephalus larva has been used by Greenwood *et al.* (1966) as a feature relating the Elopiformes, Anguilliformes and Notacanthiformes as a distinct, natural lineage.

A note of caution must be introduced here since it is not certain whether the development of the leptocephalus is a specialized condition or if it is simply another feature retained from halecostome ancestors. Harrisson (1966) and Romer (1966) both imply that the leptocephalus is a retentional feature, but give no evidence for this.

A leptocephalus occurs in three orders (also linked by other intergroup characteristics, Greenwood *et al.* 1966) which are anatomically, ecologically and biologically diverse. Yet it is present in these three orders only. The absence of a leptocephalus, or anything approaching such an ontogenetic stage, in clupeomorphs, osteoglossomorphs or protacanthopterygians is perhaps the strongest argument for assuming that this larva evolved only within the elopiforms. Furthermore, the peculiarities of the leptocephalus suggest that it arose but once and must have been present in early Cretaceous times, before the elopoid–albuloid dichotomy. In short, circumstantial evidence is in favour of the leptocephalus being an elopiform specialization subsequently inherited by the eels and notacanths (+ halosaurs and lipogenyids).

If, in the future, it should be demonstrated that the leptocephalus is a primitive or retained feature then its use as an indicator of interordinal relationship will no longer be valid and it will have to be added to the already long list of elopiform characters that have been inherited from halecostome ancestors.

A second feature that is here assumed to be an elopiform development is the possession of rostral ossicles. The snout of teleosts appears to be very labile, subject to many modifications related to feeding mechanisms. The sensory canals and associated ossifications are no less labile and may be seen to vary considerably both between and within each family. Within the Elopiformes, variation in the sensory canals of the snout has involved the movement, loss, or even multiplication of rostral ossicles, the existence of which is unique to the Elopiformes and Notacanthiformes.

The origin of rostral ossicles as seen in *Elops* has been discussed by Nybelin (1956, 1967a), who suggested that they arose by fragmentation of the dermethmoid (rostral

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[2] (Added in proof.) Jessen (1972) has since published an excellent study of the pectoral girdle and fin of actinopterygians. Jessen suggests that the pectoral splint is a fin-ray derivative and is a primitive character, being found (in a more primitive state) in *Lepisosteus* and *Amia*. Jessen's conclusions are accepted here. The presence of a pectoral splint in elopiforms must therefore be regarded as of little use in linking elopoids with albuloids. The pectoral splint is nevertheless diagnostic for elopoids and albuloids among teleostean fishes. The present author knows of no other teleost with a pectoral splint, implying that neither elopoids nor albuloids could have been derived from known teleosteans.

of Nybelin *op. cit.*, producing the lateral rostral ossicle) and the antorbital (producing an additional ossicle). Although there may be a prenasal ossicle incorporated in the dorsal part of the lateral rostral ossicle (Nybelin 1967a : fig. 2), there is never any connection between the supraorbital and ethmoid commissure sensory canals.

Megalopids differ little from the *Elops* condition, the most significant difference being the loss of the anterior fragment of the antorbital. According to Gosline (1961 : 22) the loss of this ossicle has been accompanied by the loss of a small section of the canal and thus the ethmoid commissure fails to connect with the infraorbital system. Nybelin (1967a), however, finds a connection in the soft tissue of *Megalops* and young *Tarpon*. Following Nybelin's technique of ink injection I find a connection in *Megalops* and *Tarpon* (the largest *Tarpon* examined in this respect was of 222 mm S.L.). A difference from the *Elops* condition is the very close relationship between the lateral rostral ossicle and the premaxilla. In young *Megalops* and *Tarpon* the ossicle is clear of the premaxilla (Nybelin 1967a : fig. 2), but in older specimens of these genera the rostral ossicle comes to lie in a shallow excavation on the lateral surface of the premaxilla, and is very tightly bound to that bone.

While reduction in the number of canal bearing bones may be a feature of the megalopids, multiplication is characteristic of the albuloids. Thus *Pterothrissus* has three ossicles, although it is impossible to be sure which are dermethmoid derivatives and which are antorbital in origin. It is suspected that the fossil albuloids had more than three ossicles since the development of the premaxillary canal was probably mediated by a morphological stage such as is seen in Recent halosaurs (Notacanthiformes).

The development of the snout canal system of albuloids is hypothesized to have taken the following course. From a basal albuloid such as *Osmeroides* (which has an ethmoid commissure very much like that of *Elops*, other ossicles being unknown), the anterior end of the dermethmoid turned ventrally through 90° taking the rostral ossicles with it. The rostral ossicles subsequently fragmented into several smaller ossicles, some of which lay in the skin over the premaxilla. Such a stage may be seen in the halosaurs *Halosaurus* and *Halosauropsis*, where there are four to seven ossicles forming a chain across the snout, each ossicle apparently associated with a neuromast (Gosline 1961). In albulids and pterothrissids those ossicles overlying the premaxilla became closely associated with that bone (as in *Tarpon*) and eventually fused with it, producing the condition seen in the albulids and pterothrissids where the sensory canal appears to pass through the premaxilla. The premaxillary canal is supplied by a branch of the buccal nerve (indicating its relationship with the infraorbital canal) which pierces the premaxilla close to the point of articulation of that bone with the ethmoid. The ethmoid commissure may still be continuous in some halosaurs (Gosline 1961), but it is broken in the mid-line in Recent albuloids, presumably by the loss of a median portion. It appears that in this assemblage (albuloids and halosaurs) the ethmoid commissure has shifted its association from the dermethmoid to the premaxillae.

The retention of the originally continuous ethmoid commissure–infraorbital canal system in the Elopiformes is probably a consequence of the solid snout of these fishes. In other groups, notably clupeiforms, salmoniforms and cypriniforms, the movement of the premaxilla and maxilla is such that a delicate sensory canal would be stretched and broken. The isolated ethmoid commissure remains as a superficial line of pores within the skin of many ' lower ' teleosts (Nybelin 1967a).

The Elopiformes are traditionally linked with the Clupeiformes (Denticipitoidei and Clupeoidei) (Regan 1909 ; Berg 1940 ; Bertin & Arambourg 1958). As suggested by Greenwood *et al.* (1966) there is little evidence to support this proposal. If a relationship exists it is probably to be found below the teleost level.

Clupeiform anatomy has been influenced by the following trends :

a. Development of an otophysic connection involving an intimate intracranial association between the swimbladder and the inner ear.
b. Development of a recessus lateralis, and elaboration of the sensory canal system on the cranial bones. This is often accompanied by the loss of a well-defined lateral line canal on the trunk.
c. Development of a temporal foramen between the frontal and parietal which houses a region of sensory tissue, the ' sinus temporalis ' (see Patterson 1970a for a discussion of this sensory tissue).
d. Deepening of the suspensorium with an increasing mobility of the dermal jaw elements, particularly the supramaxillae. (The engraulids and chirocentrids are exceptional in this respect ; *Denticeps* has no supramaxillae, Greenwood 1968).
e. Development of microphagous feeding habits (except *Chirocentrus*) which principally involves reduction or loss of teeth on the dermal jaws, gill arches and palate and the development of epibranchial organs (Nelson 1967).
f. Development of a unique type of caudal skeleton, characterized by a free first hypural, fusion of the second hypural with the first ural centrum and fusion of the first uroneural with the first preural centrum (Gosline 1960, 1961 ; Greenwood *et al.* 1966 ; Cavender 1966). *Denticeps* is somewhat more primitive (Greenwood 1968).
g. Lateral compression of the body accompanied by the development of scutes in the ventral mid-line (a few also show dorsal scutes, e.g. *Diplomystus*, *Hyperlophus* and *Potamalosa*).

These clupeiform trends are quite distinct from any seen in the elopiforms. In those elopiforms with an otophysic connection (Megalopidae) it is entirely extracranial and involves hypertrophy of the intercalar, an element which in clupeomorphs is reduced to a tiny cap of bone. Lateral compression of the body, also seen in the megalopids, is never associated with the development of scutes.

The Upper Cretaceous species of *Diplomystus* are in many respects the most primitive clupeiforms known (Patterson 1967a). A derivation of *Diplomystus* from a basal elopiform, such as the Upper Jurassic *Anaethalion vidali*, is unlikely in view of the fact that *Diplomystus* has retained a basipterygoid process and a heavily ossified mesethmoid (for the primitive and advanced condition of the ethmoid elements see Patterson 1970b). Conversely, elopiforms could not have been derived from a *Diplomystus*-like clupeoid since the latter is already specialized towards the clupeoid condition in showing pre-epiotic fossae, a specialized path of the supratemporal commissure and certain specializations of the tail (Patterson 1967a : fig. 8 ; Greenwood 1968 : fig. 32 ; Cavender 1966 : fig. 4).

Thus it is improbable that clupeiforms were derived from known elopiforms or *vice versa*. However, this does not rule out the possibility that these two orders shared a common ancestor above the pholidophorid level, within the teleosts. The ancestry of clupeiforms is obscure. Prior to the Albian no teleost is known to possess any of the primary clupeiform cranial characters (for these, see Patterson 1970a). Despite this, both the Clupavidae and the Leptolepididae have been considered ancestral to the clupeiforms (Arambourg 1950, 1954).

Recently, Patterson (1970b) has indicated that the Clupavidae is a heterogeneous assemblage containing many poorly known forms. Those species which may be referred to the Clupavidae with any degree of certainty show a fusion of the first ural centrum with the first preural centrum (Patterson, *op. cit.*), a feature only found among euteleosteans.

This leaves the leptolepids as candidates for clupeiform ancestors. A suggested leptolepid–clupeiform relationship is based upon gross similarities of jaw, trunk and fin shape (Arambourg 1950, 1954). At present there is no firm evidence that the leptolepids are involved in the ancestry of the clupeiform fishes, yet there is no reason to reject such a suggestion.

The leptolepids could not have been ancestral to the elopiforms, since the latter are more primitive in showing a dermethmoid which is separate from the mesethmoid. In leptolepids the dermethmoid is fused with the mesethmoid. On the other hand, elopiforms are more specialized than leptolepids in possessing a supraorbital-infraorbital sensory canal connection and in lacking a basipterygoid process. There is no known teleost primitive enough to be considered ancestral to both the elopiforms and the leptolepids or to the elopiforms and the clupeiforms.

In short, it is very unlikely that the elopiforms and the leptolepids are related above the pholidophorid level and it is even more unlikely that the elopiforms and the clupeiforms are related within the Teleostei.

Members of the Elopiformes have at one time or another been considered related to members of the Osteoglossomorpha (following the work of Patterson 1967c, the plethodonts are included in this assemblage : the ichthyodectids are also considered related to osteoglossomorphs, Greenwood *et al.* 1966 ; Patterson 1967c). It is unlikely that such a relationship exists within the Teleostei.

Garstang (1931) suggested a relationship between the Elopoidei and the Hyodontoidei + Mormyroidei on the basis that at least some members of all three groups show the development of an otophysic connection and a similarity in the opposition of parasphenoid and basihyal teeth. However, the type of otophysic connection is very different in the two groups and was probably developed independently. The similarity in buccal occlusion may be explained as the retention of a primitive feature, such as is found in pholidophorids, and is therefore of little use in indicating relationship.

Woodward (1901) related the Osteoglossidae and Plethodontidae to the Albulidae, mainly on the basis of the powerful buccal dentition seen in these families. In view of the great dissimilarities in the pattern of the roofing bones, infraorbital bones, vertebral column and caudal skeleton, the albulids appear far removed from these osteoglossomorph fishes (see also p. 207).

Bardack (1965) suggests that the plethodonts were derived from elopoids but the reasons given do not stand critical examination. The similarity in dentition is a convergent development (p. 207), the similarity in neurocranial architecture is merely due to primitive characters (flat roof, medially united parietals and roofed post-temporal fossae), and the common possession of an ossified interorbital septum is again an example of convergence to meet a similar functional need.

The osteoglossomorphs are anatomically diverse, but the evolutionary trends which have influenced osteoglossomorph anatomy are quite distinct from those manifest in the elopiform complex. The osteoglossomorphs show :

a. The development (in the vast majority) of a predatory method of feeding which is imposed upon the basic teleostean parasphenoid-basibranchial/basihyal bite. This trend has resulted in a relatively immobile palate and upper jaw and the retention of both a basipterygoid process and a well-ossified ethmoid region (for a fuller discussion of osteoglossomorph jaw adaptations see Greenwood *et al.* 1966).
b. Development of an otophysic connection in some ; but this is never developed in either the megalopid or the clupeomorph fashion (Greenwood 1963).
c. Reduction and consolidation of the circumorbital elements (Nelson 1969b).
d. Close association between the upper jaw and the infraorbitals.
e. Development of a unique type of caudal skeleton (Greenwood 1966 ; Cavender 1966 ; Nelson 1969b) which can only be derived from the type found in Liassic leptolepids or pholidophorids.

The diversity of the Osteoglossomorpha makes overall comparison with the elopiforms difficult, but in none of the osteoglossomorph groups are there significant features with counterparts in the elopiforms (for Ichthyodectidae see Bardack 1965 ; for Tselfatioidei see Patterson 1967c ; for Osteoglossiformes and Mormyriformes see Greenwood 1966 and Greenwood *et al.* 1966).

Palaeontological evidence suggests that the osteoglossomorph complex is an ancient one ; the Hiodontoidei are first known from the Upper Jurassic (Greenwood 1970b), the highly specialized Tselfatioidei from the Albian, and the Ichthyodectidae are recorded from the Tithonian (possibly as early as the Oxfordian, Bardack 1965).

Ichthyodectids such as *Allothrissops* from the Kimmeridgian, and *Thrissops* from the Oxfordian appear to be the least specialized osteoglossomorph fishes. Even in these forms, however, there are features which militate against their having been derived from, or having given rise to, elopiform fishes. *Allothrissops*, for instance, is more specialized than elopiforms in showing a reduced supratemporal, a reduction in the size of the antorbital and a restricted parasphenoid dentition. It also apparently shows no distinct dermethmoid element (Patterson 1967a : fig. 2). The supraorbital–infraorbital canal connection of *Allothrissops* is developed in a different way from that seen in elopiforms. In *Allothrissops* the connection is indirect, *via* the otic sensory canal, whereas in elopiforms it is direct.

Specialized features of primitive elopiforms which rule out their being considered ancestral to *Allothrissops* and related teleosts include : loss of the basipterygoid process, reduction in snout ossification, reduction of branching of the preopercular canal, and the more advanced type of caudal skeleton in which there is a differentiation of the uroneural series (p. 91).

Between the remainder of the osteoglossomorphs and the elopiforms there is an even greater 'incompatibility' of specialized features, particularly in aspects of caudal anatomy. In short, the present state of palaeontological knowledge suggests that the osteoglossomorphs and the elopiforms are not related above the pholidophorid level.

A comparison between the Elopiformes and primitive members of the Euteleostei (salmonoids, osmeroids, esocoids, argentinoids, chanoids and gonorynchoids) is difficult since the early history of euteleosteans is very poorly known. That all euteleostean fishes were derived from a single teleost ancestor has yet to be demonstrated, and the relationships between the primitive euteleosteans mentioned above are not clear. It seems certain, however, that the euteleostean complex is an ancient one since specialized members occur in Cenomanian times (Goody 1969b; Patterson 1967b). In view of the uncertainty concerning the origin and early evolution of the euteleosteans, remarks will at this stage be kept brief.

Elopiformes and each of the euteleostean groups appear divergently specialized and any relationship of ancestor–descendant type between these two groups appears impossible. However, the possibility of there having been an ancestor common to the elopiforms and the euteleosteans cannot be ruled out.

In this connection the Upper Jurassic *Anaethalion* is of interest. The anatomy of *Anaethalion* is poorly known, particularly with respect to cranial details. One of the contained species, *A. vidali* from the Kimmeridgian of Spain, shows a pectoral splint bone and is thus referred to the Elopidae (p. 36). I have examined a few specimens of the species described by Nybelin (1967b) and am unable to determine the presence or absence of a comparable splint bone in the Bavarian forms. For the time being therefore the systematic position of most *Anaethalion* species must remain *in limbo* (see also pp. 35–44). I would, however, like to draw attention to certain features of the caudal skeleton of the genus.

The tail of many euteleostean fishes shows several distinctive features. Firstly, the last few neural and haemal spines show the development of median expansions of laminar bone (Patterson 1970b; Greenwood & Rosen 1971). Secondly, in some euteleosts, there are well-developed neural arches associated with the first preural and first ural centra, which in these fishes may fuse with the first uroneural forming the stegural (Paterson 1970b). The fate of these neural arches varies during the evolution of different euteleostean lineages (for a discussion of the primitive euteleostean tail see Patterson 1970b). Thirdly, the epural series of euteleosteans is composed of two or three epurals which are usually of equal length, unlike the graded series seen in the caudal skeleton of elopiforms.

Within the genus *Anaethalion* these 'euteleostean' features are variously developed. Two forms mentioned by Nybelin (1967b), *A.* (?) cf. *subovatus* and *A.* sp. ('*Elops*-ähnlicher Fisch', Nybelin 1963, 1971) show few of the above features. *A. angustissimus* shows laminar bone, moderately well developed neural arches and epurals of equal length (Text-fig. 18C, Nybelin 1971). *A. knorri* (Text-fig. 18D, Nybelin, 1971) and *A. angustus* (Text-fig. 18B) both show laminar bone, but the neural arch associated with the first preural centrum is poorly developed (the neural arch of the first ural centrum is not known). The epurals of these two species are of unequal length and form a graded series.

Significantly, the elopiform *Anaethalion vidali* shows the development of laminar bone and moderately expanded neural arches associated with the first preural and ural centra, but the epurals form a graded series (Text-fig. 17).

Anaethalion cannot be regarded as ancestral to both the elopiforms and euteleosteans (assuming the latter to be monophyletic) since there are euteleosts such as alepocephaloids and the osmerid-like *Humbertia* more primitive than *Anaethalion* in possessing a basipterygoid process (for alepocephaloids see Gosline 1969; for *Humbertia* see Patterson 1970b).

Considering the similarity between the caudal skeleton of primitive elopiforms and euteleosts, there are two conclusions to be drawn. Either the development of laminar bone has little significance in indicating relationship, having been developed in parallel, or a true relationship exists, beneath the *Anaethalion* level, from an ancestor very similar to *Anaethalion* in which there was a basipterygoid process.

In summary, the Elopiformes show no relationship with either the Clupeomorpha or the Osteoglossomorpha above the pholidophorid level. A relationship with the euteleosts is suggested by the caudal anatomy of *Anaethalion* but definite evidence is lacking.

The order Elopiformes is constituted by two radically different suborders, the Elopoidei and the Albuloidei. Each suborder shows trends not seen in the other, and it is difficult to discern any trend common to both. The elopoids retain the greatest number of primitive characters and appear in the fossil record well before the albuloids. On these criteria (and see below) the albuloids are considered to have evolved from the elopoids.

Albuloids may be traced back to the Albian, where they are represented by *Osmeroides lewesiensis*, a form that exhibits an essentially albuloid neurocranium but resembles elopids rather than other albuloids in many primitive features (e.g. 48, 49, 50, 51, 55, 56, 58, 59, 60, 62, 63, 68 and possibly 69 from the list on p. 189). The dichotomy between the albuloids and the elopoids must therefore have taken place at some time prior to the mid-Albian. Within the elopoids only the primitive Elopidae could have been ancestral to the albuloids. The other elopoid family, the Megalopidae, shows trends very different from those seen in albuloids, such as deepening of the head and body, enlarged scales, enlarged post-temporal fossae and the development of an otophysic connection.

(c) *Suborder Elopoidei*

The suborder Elopoidei consists of the conservative Elopidae and the more specialized Megalopidae. Opinion is divided as to whether all elopoids should be grouped in a single family or whether to recognize two families, as is done here. Many authors, writing from a primarily neontological standpoint, recognize a single family, the Elopidae (Boulenger 1910; Barnard 1925; Fowler 1936; Bertin & Arambourg 1958; Okada 1960; Hildebrand 1963). Hildebrand (1963) speaks against separate family status for *Elops* on the one hand and *Megalops* (and *Tarpon*) on the other, quoting similarities in primitive characters (gular plate, numerous branchiostegals, large maxillaries, etc.) to support his argument. Others have adopted the families Elopidae and Megalopidae (e.g. Jordan 1923; Berg 1940; Danil'chenko 1964; Romer 1966). It is perhaps significant that these latter authors considered both fossil and Recent forms. Fishes grouped here as megalopids have a long history, extending back at least to the Albian. Furthermore, megalopids show several specializations of long standing that would not be appreciated by including the megalopids with the elopids. Therefore, in recognition of the long separate history and the fact that the megalopids show several specializations not seen in the Elopidae, the megalopids are accorded separate familial status.

The Elopidae, the most primitive of the Elopiformes, are represented by *Elops*, *Davichthys* and at least one species of *Anaethalion* (*A. vidali*). The primitive nature of *Elops* has been stressed by many authors and both Saint-Seine (1949) and Nybelin (1956) have suggested that *Elops* is a halecostome. This view has little to support it. Firstly, *Elops* shows basic teleostean features such as perichordally ossified centra, fin-rays of the lower caudal lobe that are supported by two hypurals which articulate with a single centrum, modification of the ural neural arches to form uroneurals (these caudal features have been used by Patterson 1967a, 1968a to define the Teleostei), the development of a complete lateral commissure, and narial openings which are situated close together and distinct from the nasal bone. Secondly, to include *Elops* in the Halecostomi would result in all elopiforms, notacanthiforms and anguilliforms also being considered as halecostomes and the term teleost would, in consequence, have little meaning.

The Elopidae are recognized as a group distinct from other elopiforms by the absence of specializations. This is clearly an unsatisfactory situation but one that is very difficult to rectify. Trends within the fishes grouped here are few and minor: the snout becomes slightly longer, with a resulting increase in the length of the dermethmoid; the quadrate/mandibular articulation shifts slightly posteriorly with a corresponding slight increase in mandibular length; the first infraorbital develops an ascending limb which reaches the supraorbital and thus excludes the antorbital from the orbital margin; the preopercular sensory canal moves nearer to the anterior margin of the bone and there is a reduction in branching of the infraorbital and preopercular sensory canals. A reduction in the branching of the sensory canals is seen in all elopiforms and the upward growth of the first infraorbital is seen in megalopids.

Elops itself cannot be ancestral to any other elopiform since it lacks fringing fulcra (present in megalopids and early albulids) and the ventro-lateral projections associated with the dermethmoid (present in megalopids). *Davichthys*, from the Cenomanian and Upper Santonian, retains these primitive features, but occurs too late in time to be considered ancestral to either the megalopids or the albuloids, since both the latter groups must have originated prior to the Albian. Interest thus centres on *Anaethalion vidali*, an Upper Jurassic elopid, which does show certain features normally associated with the megalopids (see p. 42).

The Megalopidae contains six (possibly seven) genera which show distinct specializations. The differences between the megalopids and their closest relatives, the elopids, are given below (Table I). In all these features the megalopids are more specialized.

TABLE I

Differences between the Elopidae and the Megalopidae

Character	*Elopidae*	*Megalopidae*
i. Body	Rounded	Compressed
ii. Neurocranium	Shallow	Deepened
iii. Quadrate/mandibular articulation	Behind level of eye	Beneath eye
iv. Middle pit-line	Present	Absent
v. Autosphenotic spine	Weakly developed	Well-developed
vi. Epiotic process	Weakly developed	Well-developed
vii. Post-temporal fossae	Reaching anteriorly to the level of the autosphenotic ; never confluent	Reaching anteriorly to the level of the orbitosphenoid ; confluent in those that can be examined in this respect
viii. Intercalar	Moderately large	Large and of complex shape
ix. Otophysic connection	Absent	Present
x. Rostral ossicles	Two	One, representing the more anterior of elopids
xi. Pelvic fins	Originating beneath or posterior to the dorsal fin	Originating beneath or anterior to the dorsal fin
xii. Anal fin	Short based, first pterygiophore short	Long based, first pterygiophore long
xiii. Scales	Lateral line tubes unbranched	Lateral line tubes branched

Trends within the Megalopidae include : the enlargement of the post-temporal fossae with a corresponding increase in the convexity of the skull roof ; reduction of parasphenoid teeth ; the development of a superior mouth and the development of a large coronoid process on the mandible.

The megalopid neurocranium has been modified in response to the forward extension of the swimbladder and epaxial musculature. In primitive teleosts the bulk of the epaxial musculature extends forwards into paired post-temporal fossae whose anterior wall is formed by the autosphenotic of either side. In Recent megalopids these fossae have become enlarged so that the anterior wall of the fossa is formed by the orbitosphenoid and the fossae of either side are confluent above the cranial vault. The vertical depth of these fossae has also increased resulting in greater convexity of the skull roof in the otic region. Many teleosts have retained post-temporal fossae, but the enlargement of these vacuities is a feature unique to the megalopids. Some other groups, e.g. salmonids and ichthyodectids, have supplemented the post-temporal fossae by the development of grooves upon the roof, while a general tendency among clupeomorphs and more advanced protacanthopterygians is to erode the roof so producing a post-temporal groove.

The otophysic connection of the Megalopidae is of a simple type, totally unlike that found in other groups possessing a swimbladder–cranial linkage (clupeomorphs, notopteroids and juvenile mormyriforms, Greenwood *et al.* 1966). Although the megalopid otophysic connection was probably derived from a basic type (see footnote, p. 189) common to the other groups mentioned, its subsequent development has followed a different and restricted path. There is never any direct connection between the swimbladder and the endocranial cavity and the association of the precoelomic diverticulum with the intercalar is unique.

There are several minor osteological and soft anatomical differences between the otophysic connection of *Megalops* and *Tarpon* (Greenwood 1970a), but there is nothing to suggest that both types were not derived from a common ancestral type very much like that of *Tarpon*. The Eocene megalopids exhibit a simple type of otophysic connection in which the lateral cranial wall has a single large depression for the swollen end of the swimbladder, which presumably lay against the skull at this point as in *Tarpon*. The diverticulum could not have been as closely associated with the cranium as it is in the Recent megalopids since the vagus foramen, the glossopharyngeal foramen and the posterior opening of the jugular canal still occupy primitive positions. In the Recent megalopids the nerve foramina have moved to allow the swimbladder to fit tightly under the intercalar. Thus in both *Tarpon* and *Megalops* the glossopharyngeal leaves the neurocranium immediately beneath the vagus and slightly behind the level of the intercalar. The posterior opening of the jugular canal has moved upwards, so much so in *Megalops* that it opens directly into the subtemporal fossa, and the head vein has acquired a different spatial relationship to the intercalar (see p. 67).

The intercalar of the Recent megalopids has been described in detail by Greenwood (1970a) and shown to be more complex in *Megalops* than in *Tarpon*. However, in both there is a lower intercalar limb associated with the swimbladder diverticulum. Specimens of the Eocene megalopids do not show a lower intercalar limb yet it is assumed that one was present and that it was developed much as in young *Tarpon* (see Greenwood 1970a). If the lower intercalar limb was absent in the Eocene species one would be forced to recognize that an identical intercalar development had taken place twice, a view with little to recommend it. A lower intercalar limb must have been present in *Protarpon* as well as in *Promegalops* since the latter has a neurocranium more like that of the more specialized *Megalops* than *Tarpon*. The apparent absence of the lower intercalar limb in the fossil representatives is not surprising in view of the fragility of the pedicel connecting the lower limb to the main body of the intercalar.

The caudal anatomy of the Megalopidae is primitive and essentially similar to the *Elops*-type. Loss of the urodermal is derived relative to the *Elops* condition, but the retention of fringing fulcra is primitive.

Fringing fulcra are rare among teleosts. Besides the Megalopidae, fringing fulcra are known in *Leptolepis* (Leptolepididae), *Lebonichthys* (Albulidae), *Anaethalion* (? Elopidae) and *Davichthys* (Elopidae). All members of the Megalopidae in which the caudal fin is known show fringing fulcra. Fringing fulcra in teleosts are confined to the region above the uppermost principal caudal ray, and, except in *Sedenhorstia* and older specimens of *Megalops*, only one or two are usually present.

In the teleosts mentioned above, the upper principal caudal ray is preceded by a number of fringing fulcra in front of which lie a number of fin-rays variously termed epaxial fin-rays (Gardiner 1970), raylets (Hollister 1936; this term applied to those rays which are not articulated), accessory rays (Goody 1969b), procurrent rays (Patterson 1968b) or basal fulcra (Patterson 1968a). Irrespective of terminology, these rays, which are supported by epurals or neural spines, appear to represent fringing fulcra that have migrated downwards (Gardiner 1970). In support of this interpretation is the fact that, in most lineages, fringing fulcra occur prior to epaxial rays, the exception being the pholidopleurid *Australosomus*.

It is hypothesized that in the primitive actinopterygian tail there were no fin-rays above the axis of the notochord. All rays now found in this position are derived from fringing fulcra that have moved down and forwards. The downward movement of fringing fulcra has occurred in the lineages leading to the pholidopleurids, pycnodonts, perleidids, pachycormids, amioids and teleosts, and in all instances it is associated with tail shortening. Having moved down, the fringing fulcra become basal fulcra (epaxial fin-rays, etc....), supported by endochondral elements. Subsequent elongation of the basal fulcra produces the need for articulation. *Megalops* and *Tarpon* are unusual among teleosts retaining fringing fulcra in having articulated basal fulcra, although a great many teleosts without fringing fulcra have articulated basal fulcra.

A more vexatious problem concerns the origin of the fringing fulcra themselves. Reasonable suggestions as to their origin fall into three categories: firstly, derivation from the median scale row; secondly, derivation from the repeated unilateral dichotomy of the leading fin-ray; thirdly, breaking up of the articulated leading ray. For the first hypothesis there is little evidence. A median scale row would form an equally effective cutwater as a fulcral element formed of two lateral halves, and there is no reason to believe that scales broke into lateral halves.

The second hypothesis, that fringing fulcra arose by unilateral dichotomy of the leading fin-ray, was suggested by Gardiner (1970). Such a development followed loss of the cutwater previously provided by the median scale row and the scaled body lobe of the tail. That fringing fulcra are not found in early actinopterygians with unbranched fin-rays supports this view. Furthermore, the first occurrence of caudal fringing fulcra is concurrent with the first occurrence of caudal ray branching (*Stegotrachelus finlayi*, upper Middle Devonian of Scotland). However, if fringing fulcra were formed by branching of the leading ray, numerical correspondence would be expected between the fulcra and the segments of the supporting ray. Ideally, one fulcrum would be associated with one articulation. This is certainly not the case in the Elonichthyidae (Gardiner 1970), and in a range of genera examined there was never any constant numerical relationship between the fulcra and the articulations of the supporting ray. One final point is that the number of fulcra would be fixed at an early ontogenetic stage, when, although not necessarily ossified, the rays exhibit the adult branched condition (observations on young *Tarpon*).

In *Megalops* (and to a lesser extent in *Tarpon*) the number of caudal fringing fulcra increases throughout the life of the individual (Text-fig. 34), long after the caudal rays have ossified. Furthermore, the ray immediately anterior to the uppermost principal in *Megalops* shows articulations which lie at an increasingly oblique angle distally; it is possible that the posterior articulations become separated as fringing fulcra. This is the third hypothesis mentioned above. It is interesting to note that in some pholidophorids (*Pholidophorus bechei* and *Pholidolepis dorsetensis*, see Patterson 1968a) there is a reduced ray which lies at the base of the fringing fulcral series and which perhaps represents the basal articulation of a ray which has fragmented distally into many fringing fulcra.

A distinctive feature of both *Megalops* and *Tarpon* is the elongate last ray of the dorsal fin. This feature is of little use in indicating relationships since it has developed in *Dorosoma* and *Opisthonema* (Clupeidae) and also in the albulid *Dixonina*. In *Tarpon* and *Megalops* the growth of this terminal filament shows positive allometry. The independent development of the terminal filament in the three groups of fishes mentioned may have functional significance. The dorsal fin-rays of *Megalops* and *Tarpon* are relatively immobile, with a weak basal musculature. Most of the rays are oval in cross-section but in the last ray the filament is ' T '-shaped with the stem of the ' T ' directed anteriorly. The wings of the ' T ' are broad, particularly at the base of the ray, and extend laterally from the plane of the fin. When erect, this filament will produce turbulence resulting in drag opposing the forward momentum of the fish. I suggest that the flexible filament is forced to a nearly horizontal position when the fish is swimming rapidly, with the water pressure acting against the erector muscles. In this horizontal position the filament would produce minimum drag. As the speed of the fish decreases the filament will become more vertical, producing a drag component which is located behind the centre of gravity. In this position the drag would be useful in aiding the fish to decelerate before the flexure of the body and caudal fin allow the animal to turn.

Lineages within the Megalopidae. Sedenhorstia stands apart from other megalopids in both primitive and advanced characters. The primitive characters include the small scales, simple dorsal fin without an elongated terminal filament, and shallow lower jaw without a prominent coronoid process. Specialized features include the dentition, which is represented by a single row of teeth in the upper and lower jaws, the ossifications within the dorsal ligament, and fusion of the neural arches associated with the first preural and first ural centra. Such specializations, although few and minor, divorce *Sedenhorstia* from the ancestry of Eocene megalopids. Furthermore, *Sedenhorstia* occurs too late (Cenomanian–Campanian) to be ancestral to a more ' typical ' megalopid such as *Elopoides*.

The Albian *Elopoides* exhibits no specializations that would preclude it from consideration as an ancestor to the later megalopids. The depth of the cranium and the steep profile of the skull roof suggest that the post-temporal fossae were already large in this form, and the megalopid nature of the dentary, maxilla and scales is evident. Mention was made above (p. 85) of the apparent resemblance of *Elopoides* to *Megalops* rather than *Tarpon*, particularly with respect to the depth of the cranium and the large orbit. These features may be interrelated as a function of the absolute size of the fish. A small fish may be expected to have a relatively large eye, and hence a greater bulk of eye musculature accommodated within a deepened myodome. This, in turn, would effectively reduce the depth of the branchial chamber. To compensate, the suspensorium became deeper. Thus the apparent resemblance to *Megalops* may not have phyletic significance in this particular case. In other features *Elopoides* may be considered ancestral to either or both of the Eocene megalopids.

Of the Eocene megalopids, *Protarpon* and *Promegalops*, the former is more primitive and resembles *Tarpon*. *Promegalops* is closely related to *Megalops*, the similarities including the shape of the neurocranium and the position of the lower jaw articulation. Whether *Promegalops* is more closely related to *Protarpon* or *Elopoides* is unknown, there being no evidence one way or the other.

(d) *Suborder Albuloidei*

The suborder Albuloidei consists of three families, the Albulidae, Pterothrissidae and Osmeroididae (nov.). The suborder is known in the fossil record from the Albian and is represented in the Recent fauna by three genera (*Albula*, *Dixonina* and *Pterothrissus*). The Albulidae and Pterothrissidae are very much alike, more so than either is to the stem family, the Osmeroididae, and in the discussion of the families the first two are considered together. The Osmeroididae show few of the specializations of the Albulidae or the Pterothrissidae.

Fishes grouped here as the Albulidae and Pterothrissidae have been recognized as a distinct assemblage but placed near the elopoid fishes because of the common possession of many primitive features (Ridewood 1904). The Osmeroididae, containing the genus *Osmeroides* and possibly *Dinelops*, have in the past been associated with the Elopidae (Woodward 1901 and all subsequent authors). Although *Osmeroides* does not show many albuloid specializations, it shares with these fishes a pattern of neurocranial architecture which is significantly more advanced than that of the Elopidae and completely different from that of the Megalopidae. Furthermore, within the genus *Osmeroides* can be seen the initiation of morphological trends that were to become fully expressed in both the Albulidae and the Pterothrissidae. In other words, the Osmeroididae are a link between the Elopidae on the one hand and the Albulidae and Pterothrissidae on the other. The Osmeroididae are included in the Albuloidei on the basis of neurocranial specializations.

In all albuloids the neurocranium is shallow and the subtemporal fossa is deep, extending inwards to partially occlude the post-temporal fossa. The latter is small and directed antero-medially. The sub-epiotic fossae augment the post-temporal fossae in receiving the epaxial trunk musculature. The dilatator fossae are always deep, narrow dorso-ventrally and completely roofed. In the lateral neurocranial wall there is a large ridge running across the face of the prootic which provides a point of attachment for the anterior branchial musculature. The otic bulla, containing the sacculith, is very large and precludes any possibility of there being a primitive type of otophysic connection (cf. Megalopidae). There is no prootic-intercalar bridge, indeed the intercalar is reduced in albuloids. The lateral ethmoid and parasphenoid meet, sometimes in a suture. Finally, there is a deep depression at the base of the parasphenoid ascending wing, the significance of which is not known.

Other advanced cranial characters found in nearly all albuloids are the enlarged sensory canals (developed to varying degrees throughout the group), a reduced supratemporal, resulting in the middle portion of the supratemporal commissure running in the skin, and the position of the quadrate/mandibular articulation which is always beneath the orbit or the lateral ethmoid. The trunk of albuloids is rounded and the head is nearly as broad at the occiput as it is deep.

Trends and characters seen in the more 'advanced' albuloids include the following:

i. Enlargement and modification of the sensory canals.
ii. Roof of the neurocranium with anterior ridges and troughs, particularly in the snout region, which is slightly elongated.
iii. Hyopalatine series long, shallow, with an anteriorly directed quadrate. The symplectic is large and the palatine has processes articulating with both the mesethmoid and the lateral ethmoid.
iv. Vomer reduced.
v. Mouth small, inferior and specialized for bottom feeding.
vi. Premaxilla forming much of the oral margin of the upper jaw, maxilla reduced, with its head inturned and moving independently of the 'fixed' premaxilla. A single supramaxilla.
vii. Differentiation and modification of the palatal and basibranchial dentition.
viii. Specialization of the dentition associated with the gill arches.
ix. Dentary with a strongly developed, inflected ventral border, and correlated with this a reduction in size of the gular plate which may (*Albula*) be vertical.
x. Dermal jaw dentition of fine needle-like teeth.
xi. Modification of the caudal skeleton, involving reduction in the number of epurals, hypurals and uroneurals.

The albuloid neurocranium is distinctive in showing a slightly protruding snout which, in dorsal view, is narrow and marked by ridges and troughs associated with the enlarged supraorbital sensory canal. The Osmeroididae generally have no prominent ridges on the roof but *Osmeroides latifrons* shows a neurocranial roof much like later albuloids. Enlargement of the sensory canals is seen throughout the group. In the basal *Osmeroides lewesiensis* the cephalic sensory canals run entirely within the bones, opening to the surface by pores. In *O. latifrons* the supraorbital canal opens to the surface above the lateral ethmoid and continues forward in a shallow trough, which probably also contained the nasals. In this respect this form resembles the Albulidae. In the Pterothrissidae the supraorbital canal runs within bone for a short distance only; thus in *Pterothrissus* the canal opens above the posterior half of the orbit. The otic canal of the Pterothrissidae and of *Lebonichthys* among the Albulidae is only partially covered by bone.

In the Albulidae, and to a greater extent in the Pterothrissidae, the infraorbital, mandibular and preopercular canals are only partially covered by bone. The open infraorbital canal results from the coalescence of adjacent sensory pores, a trend which is first seen in *O. latifrons*. The enlargement and opening out of the mandibular canal has also taken place within *Osmeroides*. Thus *O. lewesiensis* and *O. levis* show an intramural canal, while the only portion of the mandibular canal contained within bone in *O. latifrons* is in the articular. In both the Albulidae and the Pterothrissidae the mandibular canal lies in a shallow groove, never passing through bone. Associated with enlargement of the mandibular canal, the ventral edge of the dentary becomes inturned so that in the Albulidae and Pterothrissidae the lower margins of the rami meet in the ventral mid-line. The skin between the jaw rami is folded in the Recent albuloids and in *Albula* the gular plate, which is necessarily reduced in size, lies vertically. The Pterothrissidae have lost the gular plate.

The sensory canal system of the snout in the Albulidae and Pterothrissidae is peculiarly modified and provides a possible link with the Notacanthiformes. Primitively, as in *O. lewesiensis,* the infraorbital canal ran from the first infraorbital to the dermethmoid where it joined its partner of the opposite side through the ethmoid commissure. Although they have not been found, it is assumed that there were canal-bearing rostral ossicles between the dermethmoid and the first infraorbital in *O. lewesiensis.* In the Albulidae and Pterothrissidae the snout has turned downwards and the ethmoid commissure, no longer in its primitive position, is not a continuous transverse canal. Rather the infraorbital canal now descends through rostral ossicles on to the premaxilla. The extension of the infraorbital canal on to the premaxilla is a development unique to albuloids and notacanthiforms.

The premaxilla of *O. latifrons* is unknown but it is suspected that canals were developed on the premaxilla in this form among the Osmeroididae.

In addition to the modified infraorbital canal, in the Pterothrissidae the supraorbital sensory canals of either side unite across the dermethmoid. In *Albula* the supraorbital sensory canals are separated anteriorly by a median cavity which is isolated from the canals on either side by membrane (Gosline 1961). The similarity of this condition to that in anguilliform fishes has been noted by Gosline (1961).

In the majority of ' lower ' teleostean fishes the sensory canals open to the surface by large pores. In the Albulidae and Pterothrissidae, however, the canals are covered by taut skin perforated by many tiny pores. The canals themselves are probably filled with water and the taut skin acts like a tympanum, resonating in sympathy with impinging vibrations. With the exception of the supraorbital, otic and temporal canals, the sensory canals are directed ventro-laterally and ventrally and accord with the benthic habit of the albuloids.

There are many other fishes with a cavernous canal system. The majority are inhabitants of deep water (e.g. Macrouridae), but there are also shallow-water forms (e.g. Notopteridae). The presence of a cavernous sensory canal system is therefore not necessarily related to habitat, and while its significance (other than perhaps increasing sensitivity) is not understood, its advanced nature is undoubted.

With the slightly elongated snout and the short, anteriorly situated lower jaw, the hyopalatine apparatus of the Albulidae and Pterothrissidae has become modified. The hyopalatine series is long and shallow with the articular face of the quadrate directed anteriorly. The shifting of the quadrate/mandibular articulation has been achieved by forward displacement of the quadrate which is linked to the hyomandibular by a somewhat lengthened and flattened symplectic. The metapterygoid has come to support the symplectic. A condition very much like that seen in Recent albuloids is found in *O. latifrons* (Text-fig. 59).

A further development in the hyopalatine series of most albuloids is the large foramen between the hyomandibular and the metapterygoid, through which pass deeper fibres of the levator arcus palatini muscle. In *O. lewesiensis* and *O. latifrons,* as in the elopoids and some other teleosts, the metapterygoid bears a ridge on the medial side of which the levator arcus palatini inserts. The albuloids possessing the above mentioned foramen do not show such a ridge. The only other ' lower ' teleosts I have examined in which there is a comparable foramen are *Chaetoessus* and *Chanos*, but in these forms there is apparently no passage of musculature through this aperture.

The ectopterygoid of albulid and pterothrissid fishes is produced dorsally into a well-defined process which lies against, and supports, the flimsy infraorbital bones beneath the orbit. A comparable structure is found in most elopiforms but it never reaches the same proportions as in the albuloids. In *O. latifrons* this ectopterygoid process, although a rudimentary spine-like structure, is set in typical albuloid fashion. Elsewhere an ectopterygoid process is rare but does occur in the clupeid *Dussumieria* (Ridewood 1904).

The palatine is, as in all elopiforms, composed of distinct endoskeletal and dermal components. The former is often cartilaginous (ossified in *O. lewesiensis*) and articulates with the neurocranium at two points, anteriorly with the mesethmoid or ethmoid cartilage and posteriorly with the lateral ethmoid. Among elopiforms, the lateral ethmoid projection of the palatine is only found in albuloids. Such a palatine-neurocranial connection gives some rigidity to the palate. Elsewhere, a close and rigid juxtaposition of palatine and lateral ethmoid is found in predatory fishes taking large prey such as the Chirocentridae and, presumably, the fossil Ichthyodectidae, and is a development in response to a strong biting force.

The upper and lower jaws of the Albulidae and Pterothrissidae are distinctive and produce an inferior mouth suitable for bottom feeding. *Osmeroides* shows a terminal mouth (the condition in *O. latifrons* is not known) while in *Lebonichthys* and *Istieus* it is only slightly inferior. The inferior mouth is produced by a combination of snout elongation and shortening of the lower jaw. Jaw teeth of later albuloids are found only on the premaxilla and dentary (a few maxillary teeth remain in *Istieus* and *Pterothrissus*) and the reduced maxilla supports a single supramaxilla.

The premaxilla is firmly bound to the ethmoid region by ligaments and is capable of only the slightest lateral movement. The head of the maxilla is turned sharply inwards and in the Albulidae and Pterothrissidae there is no separate palatine process on the maxilla as there is in the Osmeroididae and the Elopoidei. Instead, the rounded palatine head fits against the rear of the maxillary head. The maxilla of Recent albuloids is capable of limited independent movement ; only when the mouth is fully open does it enter the gape.

The dentition of the Albulidae and Pterothrissidae is significantly different from the primitive type seen in *O. lewesiensis*. In albulids and pterothrissids the dentition borne by the maxilla and the premaxilla consists of a broad band of needle-like teeth in contrast to the small villiform teeth borne by these elements in *O. lewesiensis*. The shape of the teeth of *O. latifrons* is intermediate.

The palatal dentition is different in each of the three albuloid families. The Osmeroididae are primitive in having small, villiform teeth on the parasphenoid, dermopalatine, endopterygoid, ectopterygoid, basihyal and basibranchial. The teeth of *O. lewesiensis* and *O. levis* are more or less uniform in size but those of *O. latifrons* differ both in size and shape. The albulid dentition is modified for crushing shelled invertebrates and the parasphenoid is equipped with large hemispherical teeth which are opposed by similar teeth on the basibranchial plate.

The pterothrissids have slightly enlarged, conical teeth on the parasphenoid, endopterygoid, basibranchial and basihyal tooth plates. There are generally fewer teeth than in other albuloids; indeed in *Pterothrissus* the parasphenoid teeth, although well developed, are confined to the region beneath the parasphenoid ascending wings. The difference in dentition no doubt reflects a difference in diet between the families, the albulids feeding essentially on molluscs and crabs while the Recent pterothrissids prey on the thinner shelled crustaceans. Stomach contents of *Pterothrissus gissu* taken off the coast of Japan (depth unknown) revealed an almost exclusive diet of caridean malacostracans.

Crushing dentition, of which one example is seen in the Albulidae, is of relatively rare but repeated occurrence among actinopterygians. The condition is clearly specialized and suited to fishes of a restricted ecological niche. Within the Chondrostei, such fishes as the Amphicentridae and the Bobasatraniidae have a crushing dentition principally involving occlusion between the pterygoid and coronoid teeth. *Bobasatrania* has a basibranchial plate with crushing teeth (Nelson 1969a).

In the Holostei the Pycnodontiformes (and to a lesser degree the Semionotidae) show a crushing dentition developed upon the dentary and the so called ' splenials ' (held to be the result of fusion between the articular, coronoid and splenial, Nursall 1964). Unlike the chondrostean examples, the opposing dentition in pycnodonts is borne by the enlarged vomer, which together with the parasphenoid is keyed to the stout ethmoid. These fishes generally have short jaws.

Among teleosts a crushing dentition is more often developed in various ways within the buccal cavity and pharynx. In Albulidae, Phyllodontidae and Plethodontidae the grinding dentition is upon the basibranchium and parasphenoid (sometimes also the endopterygoid). Such a development is the result of specialization involving the basic or primary teleostean bite. *Pristolepis* is unique among acanthopterygians in showing a toothed parasphenoid opposed by a crushing dentition on the basibranchial complex. However, here a secondarily enlarged basihyal is involved (Nelson 1969a).

Other teleosts exhibiting a grinding or crushing dentition show specialization of the posterior gill arch elements. Thus, some cyprinids have molariform teeth on the fifth ceratobranchials which work against a callus pad on the ventral surface of the neurocranium. The labroids have opposed upper and lower pharyngeal plates. A development of grinding teeth in the posterior part of the branchial arches is concomitant upon the possession of a protrusile jaw mechanism and mobile pharyngeals, the latter correlated with the development of retractores arcuum branchialium muscles. All these features are found in fishes which have lost the primary teleostean bite.

A crushing dentition has therefore arisen several times and in each case the teeth involved have been determined by the ' evolutionary grade ' of the fishes concerned.

Apart from the Phyllodontidae, about which very little is known, some of the plethodonts have a dentition somewhat similar to the Albulidae. This similarity has led to a suggested relationship between these two groups. Woodward (1901) placed the plethodont *Ananogmius* with the albulids and expressed doubt as to whether *Plethodus, Thryptodus* and *Pseudothryptodus* should be affiliated with the Osteoglossidae or the Albulidae. There are a great many characters suggesting that the plethodonts are in no way related to the albulids, including details of the cranial roof, infraorbitals, pectoral girdle, vertebral column and caudal skeleton. With respect to the dentition, although the teeth of plethodonts are developed on the same bones as in albulids, those that show a definite adaptation towards crushing (*Plethodus* and *Ananogmius*) have molariform teeth coalesced into enlarged dental plates with a histology resembling that of the ' tubular dentine ' of dipnoans (Patterson 1967c). This is in contrast to the well-defined, discrete teeth of albulids. Together with the many other anatomical differences, especially the trenchant differences in caudal anatomy, this suggests that the albulids are not related to the plethodonts and that the crushing dentition in these groups is a convergent development.

The dentition on the parasphenoid of albulids needs support to resist the strong upward bite. Thus it is not surprising to find an ossified interorbital septum in *Albula* and *Dixonina*. The albulid interorbital ossification is formed by ventral extension of the orbitosphenoid and the enlarged basisphenoid. The parasphenoid is further braced by sutural contact with the lateral ethmoid. A similar method of bracing the parasphenoid is seen in *O. lewesiensis*, which has an equally large parasphenoid. In this form, however, the interorbital septum is incomplete. It is interesting to note that in some plethodonts (Patterson 1967c : 227) the interorbital septum is also ossified. The sporadic occurrence of an ossified interorbital septum suggests that this character is not a good phylogenetic criterion. *O. latifrons*, which has a very broad parasphenoid, and *Lebonichthys*, in which the parasphenoid is virtually identical with that of *Albula*, both lack an ossified interorbital septum.

The branchial arches of albuloid fishes (only completely known in the Recent forms) differ from the primitive elopoid type in lacking a fifth epibranchial and in having the first suprapharyngobranchial represented by cartilage only (the second is absent in albuloids). The dentition associated with the arches is more distinctive. In the Albulidae and Pterothrissidae the basibranchial tooth plate carries a specialized dentition (see above). The dentition on the other gill arch elements consists of a few rounded tooth plates which are clothed with tiny, needle-like teeth. These tooth plates are few in number and totally unlike the elopoid condition, where the tooth plates form a continuous coating on the oral surface of the gill arches. The albuloid gill-rakers are few in number and only developed to any extent on the first branchial arch. Each gill-raker is club-shaped, the stem being narrow while the head bears a cluster of minute teeth similar to those on the tooth plates.

The dentition associated with the branchial arches of the Osmeroididae is incompletely known. The basibranchial tooth plate of *O. levis* is very much like that of *Elops* and is thus primitive. Upper pharyngeal plates of *O. latifrons* are rounded, as in albulids and pterothrissids. There is no substantial guide in the known gill arch anatomy to suggest a link between the Osmeroididae and other albuloids.

Among elopiforms the albuloids show a distinctive hyoid bar, with the upper and lower hypohyals offset, both with respect to one another and to the anterior ceratohyal. The afferent mandibular artery (which in most lower teleosts runs through both hypohyals) runs through the lower hypohyal only, before piercing the ceratohyal to emerge on the dorsal surface of that bone at the bottom of a prominent groove. The afferent mandibular artery of *Albula* is contained within the anterior ceratohyal and never passes through a hypohyal.

The paired fins, girdles, median fins and preural vertebral column of albuloids are very similar to those of other Elopiformes, retaining such characters as pelvic splint bones, autogenous neural and haemal arches and parapophyses, and both epipleural and epineural intermuscular bones. In keeping with the rounded trunk the pleural ribs tend to be short, incompletely encircling the body cavity.

Apart from the primitive caudal skeleton of *O. lewesiensis* (which differs from *Elops* only in possibly having a fourth uroneural) the albuloid tail is distinctive. There are only two uroneurals, the first of which is large and extends to the first preural centrum (in *Istieus* it just covers the second preural centrum). The second uroneural extends considerably beyond the distal tip of the first while in the Pterothrissidae the proximal end of the second uroneural lies well above the second ural centrum. There are six hypurals, one less than in elopoids. The bases of the inner fin-rays of each caudal lobe are unexpanded, unlike many primitive teleosts, including elopoids. There are many basal fulcra above and below the principal rays, and fringing fulcra are retained in *Lebonichthys*. There are minor details in which the caudal skeleton of the albulids differs from the pterothrissids and these are mentioned in the discussion of those families.

The similarity in neurocranial architecture between the Osmeroididae on the one hand and the Albulidae and Pterothrissidae on the other is held to be of paramount importance and has led to the inclusion of the Osmeroididae within the Albuloidei. The more advanced osmeroidids show trends in other cranial bones which are decidedly albuloid.

The differences between the osmeroidids and other albuloids are essentially those in which the former family is primitive. These primitive features (with respect to the other albuloids) include : a terminal mouth ; the simple maxilla, with a distinct palatine head and forming a substantial portion of the functional jaw ; the presence of two supramaxillae ; the dentition ; the sensory canal system, which is never cavernous although it may be slightly enlarged ; the ornamented cranial bones ; and the caudal skeleton (at least in *O. lewesiensis*) which has more than two uroneurals and in which the bases of the inner rays are expanded.

Osmeroides is the type osmeroidid genus and contains species known from the Albian to Coniacian of Europe and possibly Japan (Yabe & Okada 1930). *O. lewesiensis* appears to be the most primitive species, with the closely related *O. levis* and the more distant *O. latifrons* as derivatives. Of the three species, *O. latifrons* appears closest to the ancestry of both the Albulidae and Pterothrissidae.

The great similarity between the Albulidae and Pterothrissidae suggests that they were derived from a common ancestor. Important similarities have been mentioned above but may be summarized as the following : snout elongated, mouth inferior ; premaxilla with fine, needle-like teeth bearing a sensory canal and forming most of the upper jaw margin ; hyopalatine series with a long palatine, an ectopterygoid process and a hyomandibular-metapterygoid foramen ; branchial arches with a few club-shaped gill-rakers, dental plates with minute needle-like teeth ; cavernous sensory canal system ; caudal skeleton with two uroneurals and six hypurals.

The origin of these two families is to be found in the Osmeroididae. The Albulidae and Pterothrissidae differ from one another in several respects (some of which have been referred to above). Each family has retained and developed features not found in the other and these are listed in Table II.

TABLE II

Differences between the Albulidae and the Pterothrissidae

	Albulidae	*Pterothrissidae*
i.	Gular plate present	Gular plate absent
ii.	No median connection of supraorbital canals	Supraorbital canals of either side united
iii.	Parietals shorter than broad and irregular in shape	Parietals square or longer than broad and regular in shape
iv.	Interorbital septum often ossified	Interorbital septum never ossified
v.	Parasphenoid broad, sutured with lateral ethmoid	Parasphenoid narrow, not sutured with lateral ethmoid
vi.	Dentition of grinding teeth on parasphenoid and endopterygoid, opposed by basibranchial tooth plate bearing a similar dentition (basihyal tooth plate edentulous or absent)	Dentition of conical teeth on parasphenoid, endopterygoid and ectopterygoid opposed by basihyal and basibranchial tooth plates bearing a similar dentition
vii.	Maxillary teeth absent (except in *Lebonichthys lewisi*)	Maxillary teeth present
viii.	Vomer and palatine with needle-like teeth	Vomer and palatine edentulous
ix.	Infraorbitals behind eye completely covering the cheek region	Infraorbitals behind eye narrow and incompletely covering the cheek region
x.	Branchiostegals not less than 12 in number	Never more than 10 branchiostegals
xi.	Dorsal fin short (slightly elongate in *Lebonichthys*), anal short	Dorsal fin long, extending along most of back, anal slightly elongated
xii.	Caudal skeleton with complete neural spine on second preural centrum, caudal scute present above and below peduncle. Hypurals broad, narrow gap between the second and third hypurals. Usually two epurals	Caudal skeleton with a half spine on second preural centrum, no caudal scutes. Hypurals slender, large gap between second and third hypurals. Usually three epurals

Many of the above features are self-explanatory and little discussion is given here.

Some of the differences are specializations due to varying diets (features iv, v, vi) or different body form (xi). The reduction of the cheek covering (ix) in the Pterothrissidae may be related to the reputed deep-sea habit since a reduction of ossification is often noted in fishes from this environment. In features i and ii the Pterothrissidae are more advanced while the Albulidae are more advanced in features iii and vii.

Since there is a trend to reduce the dentition, the albulids may be held to be more primitive in the retention of palatine and vomerine teeth (feature viii). However, the teeth borne by these elements are needle-like and differ from the teeth in a similar position in the Osmeroididae. The vomerine teeth in albulids are raised on a short, transversely orientated pedicel to bring them on a level with the palatine teeth. Together these teeth form a complete semicircle of backwardly pointed teeth lying within a similarly shaped band of premaxillary teeth. Thus, while their retention may be primitive, their form is specialized.

The coronoid process of albulids is situated posteriorly while that in *Pterothrissus* among pterothrissids is situated anteriorly and is forwardly directed. This difference may be related to the position of the quadrate/mandibular articulation, which lies beneath the posterior half of the orbit in the Pterothrissidae and the anterior half of the orbit in the Albulidae. The anteriorly situated coronoid process in *Pterothrissus* has the same disposition with respect to the lateral ethmoid as in *Albula*, where the process is situated posteriorly. The insertion of the $A_2 + A_3$ division of the adductor mandibulae is correlated with the position of the coronoid process and it is suggested that in *Pterothrissus* the forwardly situated coronoid process has in some measure compensated for the more posterior position of the jaw articulation.

The difference between the families in the number of branchiostegal rays (feature x) may also be related to the position of the quadrate/mandibular articulation. In both *Albula* and *Pterothrissus* the jaw rami are close together in the ventral mid-line and the anterior end of the hyoid bar (Tchernavin 1953) does not extend between the jaws to any great extent. The distance between the ventral end of the hyomandibular and the rear end of the mandible is relatively greater in *Albula* than in *Pterothrissus* and the hyoid bar is longer. As the number of branchiostegal rays is proportional to the length of the attachment area (Gosline 1967) the pterothrissids would be expected to show a lower branchiostegal count.

It is of interest to note that in *Lebonichthys* (Albulidae) the large gular plate separates the jaw rami and although the jaw articulation is in the ' pterothrissid position ' the hyoid bar is long and extends well between the jaw rami. The loss, or great reduction, of the gular plate may have indirectly affected the shortening of the hyoid bar.

The Albulidae are known by representatives from the Eocene of Africa and Europe and the Upper Cretaceous of Asia and North America. All but one of these fossil representatives have been found in shallow-water deposits, which is in agreement with the habitat of the Recent *Albula vulpes*. The exception is the *Albula* from the Campanian of Alabama (Mooreville Chalk) which is reported to be a deep water deposit (Applegate 1970). The evolution of the Albulidae probably began in Albian or Lower Cenomanian times since *Lebonichthys lewisi* (Middle Cenomanian) already shows an albulid tail and well-developed hemispherical teeth within the mouth.

The Pterothrissidae are poorly represented in the fossil record, the only well known fish being *Istieus* from the Campanian of Germany. It is possible that *Hajulia* from the Middle Cenomanian of Lebanon is also a pterothrissid (see p. 152). In part this lack of a fossil record may be a consequence of the deep-water habit, which was probably adopted early in their history.

(e) *Possible albuloid derivatives*

A suggestion that the Notacanthiformes were derived from early Elopiformes was put forward by Greenwood *et al.* (1966 : 355). This suggestion was based upon the common possession of a leptocephalus larva and the presence of a bone-enclosed ethmoid commissure. Those authors further suggested that the halosaurid ethmoid commissure agreed with that of albulid fishes, stressing the presence in both of an enlarged canal system in this region. The development of such a canal system is dealt with in the general discussion of the elopomorph snout (p. 190). All that need be said here is that the development of the albuloid–notacanth snout canal system is unique, peculiar, and provides good evidence of a common origin.

Aside from the canal system there are two other specializations shared by albuloids and notacanths : the snout is slightly elongate and fragile, and the small mouth is inferior ; the maxilla has a slender inturned head and, with the premaxilla, is capable of lateral movement but very little vertical movement.

Beyond this, the notacanths are very specialized in comparison with the albuloids. Some of the specializations of notacanths are probably correlated with their deep-sea habitat. Thus the cranial bones are exceedingly thin and several are lost (autopalatine, dermosphenotic, epiotic, basisphenoid, orbitosphenoid, supraorbital, lateral ethmoid, pterosphenoid and, in the Notacanthidae, the interhyal). Other elements are reduced (interhyal, vomer).

The trend towards an anguilliform body has resulted in a very reduced caudal skeleton and a freeing of the pectoral girdle (at least in Notacanthidae) from the cranium. These and other specializations are dealt with at length by McDowell (in press). All that is intended here is to convey an idea of the extreme divergence of the notacanthiforms.

Fossil notacanthiforms are rare (in part this may be a result of their deep-sea habit) but halosaurs are known from the Campanian (*Echidnocephalus*) and are already so specialized that their halosaurid affinities are undoubted. Thus the origin of the group must have been some time previously, and the features shared with the Albulidae and the Pterothrissidae suggest that a Cenomanian age would be a reasonable estimate. The pterothrissids seem the best candidates for the ancestors of the notacanths since this group retains maxillary teeth (found in halosaurs) and the palatal dentition is not particularly specialized. The albulid dentition on the other hand is already specialized by Cenomanian times.

Cenomanian pterothrissids are rare, being questionably represented by *Hajulia*. This, together with the apparent absence in the fossil record of earlier, less specialized yet identifiable notacanthiforms, obscures the origin of the ‘ Heteromi ’. Nevertheless, a close association with the albuloids (in particular the Pterothrissidae) is strongly suspected.

(f) *Comments on the family Phyllodontidae*

The Phyllodontidae Dartevelle & Casier (1943) have been referred to the suborder Albuloidei by Estes (1969a) on the basis of similarity to *Albula* in the basibranchial tooth plate (in particular, the basibranchial scars) and the occlusion pattern with the parasphenoid.

The Phyllodontidae are related amongst themselves and distinguished from the Albulidae by having a phyllodont pattern of tooth replacement and in lacking pterygoid tooth plates (Estes 1969a : 328). Estes considers the absence of pterygoid tooth plates to be the more important of these characters.

The Albian genus *Casierius* Estes (1969b) has been placed in the Albulidae even though tooth replacement in this form is phyllodont. Estes (1969b) uses a similarity in the contours of the basibranchial plate and the presence of associated pterygoid tooth plates as justification for the inclusion of *Casierius* within the Albulidae.

It appears to the present author that *Casierius*, in showing a phyllodont dentition, is clearly related to the Phyllodontidae. To dissociate it from the phyllodonts only because it has pterygoid tooth plates (Estes 1969b) seems untenable. The potentiality to replace teeth in phyllodont fashion, either from directly beneath (Phyllodontinae) or in alternate fashion (Paralbulinae), would appear a trenchant difference from the albulids.

The first albulid appears in the Lower Cenomanian while *Casierius* is found in the Albian, and by this time it already had a wide geographical distribution indicating an earlier origin. The phyllodont dentition is clearly more specialized than the albulid type and, disregarding the time factor, a derivation of phyllodontids from albulids would appear more logical than the converse.

If albulids were present in the Lower Cretaceous it would be expected that tooth plates referable to this family should have been discovered, since these are as robust as those of the phyllodontids. One is left with three possibilities regarding the position of the phyllodontids : they were derived from the Osmeroididae separately from the Albulidae and at an earlier time ; they stand ancestral to the Albulidae ; or they evolved in parallel to the Albulidae.

It is difficult to comment on the possibility that the phyllodontids were derived from the Osmeroididae. Certainly no known osmeroidid shows a phyllodont dentition or any kind of replacement pattern comparable with the Phyllodontidae.

That the Phyllodontidae stand ancestral to the Albulidae is unlikely since the phyllodont dentition is so advantageous in grinding food that to revert to a much simpler type of dentition yet still retain a similar feeding method is unlikely.

A separate but parallel evolution of the Albulidae and the Phyllodontidae appears possible. Phyllodontids and *Casierius* are only known by tooth plates which cannot be referred to any more completely known fish. Until phyllodontid material other than tooth plates is known it is better to accept the classification within the phyllodontids as being artificial. The fact that the tooth plates belong to a fish at about the ' elopiform grade ' seems a reasonable supposition but the possibility of holostean or halecostome affinities cannot be ruled out.

V. SUMMARY

Descriptions are given of the Recent and fossil Elopiformes represented in the collections of the British Museum (Natural History). The basic systematic conclusions are as follows :

1. The Elopiformes are a primitive group of teleostean fishes distinguished from other teleostean orders by the combination of three primary characters : a

leptocephalus larva, the development of rostral ossicles and the modification of the outermost pectoral fin-ray to form a pectoral splint. The view expressed by Greenwood *et al.* (1966) that the presence of a leptocephalus larva links the Elopiformes with the Anguilliformes and Notacanthiformes is accepted here. Much work remains to be done on anguilliform relationships, particularly with respect to their being considered elopiform derivatives. Of these three orders the Elopiformes is the most primitive and represents the basal group from which the other two were derived.

2. Elopiformes are represented in the fossil record and Recent fauna by between fifteen and twenty genera. The fossil record extends back to the Upper Jurassic where the earliest member is *Anaethalion vidali*, a species which shows certain body proportions seen in the megalopid elopiforms.

The genus *Anaethalion* is held to be of considerable interest. In the present state of knowledge only one species, *A. vidali*, may be referred to the Elopiformes since it shows a pectoral splint, other species being unknown in this respect. The caudal skeletons of some species show a distinct resemblance to *Elops* while others show certain euteleostean characteristics. It may be of significance that the caudal skeleton of *Anaethalion vidali* shows laminar bone, as in euteleostean fishes. Insufficient information concerning the anatomy of the various species referred to *Anaethalion* renders a taxonomic revision premature. For this reason these species are referred to as the '*Anaethalion* generic complex'.

3. Within the Elopiformes the Elopidae is the most primitive family and is represented by *Davichthys* gen. nov., *Elops* and probably some species of *Anaethalion*. The elopids have remained virtually unchanged since the Upper Jurassic. The only trends noted are reduction in the branching of the cephalic sensory canals, loss of the ventro-lateral projections associated with the dermethmoid and loss of fringing fulcra.

4. The Megalopidae, represented by *Megalops, Tarpon, Promegalops, Protarpon* gen. nov., *Elopoides, Sedenhorstia* and possibly *Pachythrissops*, were an early derivative of the Elopidae. The chief trends characterizing this family are: the development of a superior mouth; an increase in size of the post-temporal fossae; the development of a unique type of otophysic connection; reduction of parasphenoid teeth; and certain minor modifications in the postcranial skeleton.

5. The suborder Albuloidei is known from the Albian to Recent. The most primitive albuloids are represented by the genus *Osmeroides* on which the new family Osmeroididae is based. *Osmeroides* is a link between the Elopidae on the one hand and the Albulidae and Pterothrissidae on the other. Within the genus *Osmeroides* there is seen the initiation of morphological trends that were to become fully expressed in the Albulidae and Pterothrissidae. *Osmeroides lewesiensis* is the most primitive species, showing an external morphology very much like that of the elopids. The neurocranium, however, is albuloid in such features as small antero-medially directed post-temporal fossae, sub-epiotic fossae, the absence of a prootic-intercalar bridge, a small intercalar and a deep dilatator fossa. *Osmeroides latifrons* is a more advanced species and exhibits a slightly elongated snout, opening out of the cephalic sensory canals, specialization of the dentition within the mouth and a short lower jaw with a strongly inflected ventral margin.

6. The Albulidae and Pterothrissidae are similar to one another in many advanced features such as: the pattern of sensory canals; the inferior mouth in which the immobile premaxilla is the major functional component of the upper jaw; the development of a hyopalatine series characterized by a hyomandibular-metapterygoid foramen, a flattened symplectic, a well-developed ectopterygoid process and a double articulation of the palatine with the neurocranium; certain specializations of the dentition borne by the gill arches; and loss of the seventh hypural and third uroneural in the caudal skeleton. The shared specializations indicate a common ancestry for the two families which is to be found within the Osmeroididae.

The Albulidae and the Pterothrissidae are divergently specialized in features related to different diets. Both families may be traced back to Cenomanian times.

7. The Notacanthiformes show certain similarities in snout morphology with the albuloids indicating that the albuloids may stand ancestral to that order. The Recent albuloids (the only albuloids sufficiently well known in details of snout morphology) are too specialized to be considered ancestral, but the possibility of some Cretaceous albuloid ancestry of notacanthiforms is suspected, the early pterothrissids being the most likely candidates.

8. Relationships of Elopiformes with basal groups of other cohorts are briefly reviewed. It is suggested that there is no relationship within the Teleostei between elopiforms and the Clupeomorpha or between the elopiforms and the Osteoglossomorpha. The possibility of a relationship between the elopiforms and any euteleostean group is difficult to analyse because of the sparse information available on the early evolution of the more primitive members of the Euteleostei. Attention is drawn to a few minor features of caudal anatomy seen in both euteleosts and elopiforms which may indicate the existence of a common teleostean ancestor.

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VII. REFERENCES

Agassiz, L. 1833–1844. *Recherches sur les Poissons fossiles*: 5 vols., 1420 pp., 396 pls., with supplement. Neuchâtel. (For dates of publication see Woodward and Sherborn, 1890.)

—— 1845. Rapport sur les poissons fossiles de l'argile de Londres. *Rep. Br. Ass. Advmt Sci.* York, 14 (**1844**): 279–310.

Allis, E. P. 1903. The skull and the cranial and first spinal nerves in *Scomber scomber*. *J. Morph.*, Philadelphia, **18**: 45–328, 10 pls.

Applegate, S. P. 1970. The vertebrate fauna of the Selma Formation of Alabama. *Fieldiana, Geol. Mem.*, Chicago, **3**: 383–433, 30 figs.

ARAMBOURG, C. 1950. Nouvelles observations sur les Halécostomes et l'origine des Clupeidae. *C. r. hebd. Séanc. Acad. Sci.*, Paris, **231** : 416–418, 1 fig.

—— 1952. Les Vertébrés fossiles des gisements de Phosphates. (Maroc, Algérie, Tunisie.) *Notes Mém. Serv. Mines Carte. géol. Maroc*, Rabat, **92** : 1–372, 44 pls.

—— 1954. Les poissons crétacés du Jebel Tselfat. *Notes Mém. Serv. Mines Carte. géol. Maroc*, Rabat, **118** : 1–188, 20 pls., 68 figs.

BARDACK, D. 1965. Anatomy and evolution of chirocentrid fishes. *Paleont. Contr. Univ. Kansas*, Lawrence, Vertebrata **10** : 1–88, 2 pls., 27 figs.

BARNARD, K. H. 1925. Marine Fishes of South Africa. *Ann. S. Afr. Mus.*, Cape Town, **21** : vii + 418 pp., 17 pls., 17 figs.

de BEAUFORT, L. F. 1909. Die Schwimmblase der Malacopterygier. *Morph. Jb.*, Leipzig, **39** : 526–644, 1 pl., 10 figs.

BERG, L. S. 1940. Classification of fishes both Recent and fossil (first edition, Russian with complete English translation). *Trudy Zool. Inst., Leningr.* **5**, 2 : 517 pp., 190 figs.

BERTIN, L. & ARAMBOURG, C. 1958. Superordre des Téléostéens : 2204–2500, figs. 1561–1788. In *Traité de Zoologie*, **13**, ed. Grassé, P.-P. Masson et Cie, Paris.

BIGELOW, H. B. 1963. Suborder Elopoidea. *In* Fishes of the Western North Atlantic. *Mem. Sears Fdn mar. Res.*, New Haven, **1**, 3 : xxi + 630 pp., 132 figs.

BLEEKER, P. 1859. Enumeratio specierum fiscium hucusque in Archipelago indico observatarum. *Act. Soc. Sci. Indo-Neerl.*, Batavia, **6** : 1–276.

BONAPARTE, C. L. J. L. 1846. *Osservazoni sullo stato della Zoologica in Europei in quanto ai Vertebrati nell'anno* : 1–51, 8 pls. Firenze.

BOULENGER, G. A. 1910. *Teleostei.* In *The Cambridge Natural History*, **7**, ed. Harmer and Shipley : xvii + 760 pp., 440 figs. Macmillan & Co., London.

CASIER, E. 1946. La faune ichthyologique de l'Yprésien de la Belgique. *Mém. Mus. r. Hist. nat. Belg.*, Bruxelles, **104** : 1–267, 6 pls., 18 figs.

—— 1966. *Faune ichthyologique du London Clay.* Text + Atlas : i-xiv + 496 pp., 68 pls., 82 figs. Br. Mus. (Nat. Hist.), London.

CAVENDER, T. 1966. The caudal skeleton of the Cretaceous teleosts *Xiphactinus*, *Ichthyodectes*, and *Gillicus*, and its bearing on their relationship with *Chirocentrus*. *Occ. Pap. Mus. Zool. Univ. Mich.*, Ann Arbor, **650** : 1–15, 1 pl.

COBBAN, W. A. & REESIDE, J. B. 1962. Correlation of the Cretaceous formations of the western interior of the United States. *Bull. geol. Soc. Am.*, New York, **63** : 1011–1044, 1 pl., 2 figs.

COCKERELL, T. D. A. 1912. Observations on fish scales. *Bull. Bur. Fish., Wash.*, **32** : 117–174, 52 figs., 8 pls.

—— 1933. The antiquity of *Albula*. *Copeia*, Washington : 226.

COPE, E. D. 1872. On the families of fishes of the Cretaceous formation in Kansas. *Proc. Am. phil. Soc.*, Philadelphia, **12** : 327–357.

—— 1877. On some new or little known reptiles and fishes of the Cretaceous number 3 of Kansas. *Proc. Am. phil. Soc.*, Philadelphia, **17** : 176–181.

CUVIER, G. & VALENCIENNES, M. A. 1846. *Histoire naturelle des Poissons*, **19** : 398 pp., Paris.

DANIL'CHENKO, P. T. 1964. Superorder Teleostei : 396–472, pls. 5–14. In *Osnovy Palaeontologii*, **11**, *Beschelyustnye ryby*. ed. Obruchev, D. B. Akad. Nauk SSSR., Moskva. (In Russian.)

DARTEVELLE, E. & CASIER, E. 1943. Les poissons fossiles du Bas-Congo et des regions voisines. *Ann. Mus. r. Congo belge*, Tervuren, A (3), **2**, 1 : 200 pp., 16 pls.

DAVID, L. R. 1940. Upper Cretaceous fish remains from the western border of the San Joaquin Valley, California. *Publs Carnegie Instn*, Washington, **551** : 83–112, 3 pls., 11 figs.

DAVIS, J. W. 1887. The fossil fishes of the Chalk of Mount Lebanon in Syria. *Scient. Trans. R. Dubl. Soc.*, **3**, (2) : 457–636, 25 pls.

DERSCHIED, J. M. 1924. Structure de l'organe olfactif chez les poissons. Première partie. Osteichthyes, Teleostei, Malacopterygii. *Annls Soc. r. zool. Belg.*, Bruxelles, **54** : 79–162, 26 figs.

DIXON, F. 1850. *The geology and fossils of the Tertiary and Cretaceous Formations of Sussex*: 422 pp., 40 pls. F. Dixon, London.

DUNKLE, D. H. 1940. The cranial osteology of *Notelops brama* (Agassiz), an elopid fish from the Cretaceous of Brazil. *Lloydia*, Menasha, **3**: 157–190, 9 figs.

EASTMAN, C. R. 1914. Catalog of the fossil fishes in the Carnegie Museum. Part 4. Descriptive catalog of the fossil fishes from the lithographic stone of Solenhofen, Bavaria. *Mem. Carneg. Mus.*, Pittsburg, **6**: 389–423, 17 pls.

d'ERASMO, G. 1946. L'ittiofauna cretacea dei dintorni di Comeno nel Carso Triestino. *Atti Accad. Sci. fis. mat. Napoli*, (3a) **2**, 8: 136 pp., 1 pl., 34 figs.

ESTES, R. 1969a. Studies on fossil phyllodont fishes: Interrelationships and evolution in the Phyllodontidae (Albuloidei). *Copeia*, Washington: 317–331, 8 figs.

—— 1969b. Studies on fossil phyllodont fishes: *Casierius*, a new genus of albulid from the Cretaceous of Europe and North America. *Eclogae geol. Helv.*, Basle, **62**: 751–755, 2 pls.

—— 1969c. Two new late Cretaceous fishes from Montana and Wyoming. *Breviora*, Cambridge, Mass., **335**: 1–15, 4 pls.

FOWLER, H. W. 1936. The marine fishes of West Africa, Pt I. *Bull. Am. Mus. nat. Hist.*, New York, **70**: vii + 605 pp., 275 figs.

FRITSCH, A. J. 1878. Die Reptilien und Fische der Böhmischen Kreideformation: ii + 44 pp., 66 figs., 10 pls. Prague.

GARDINER, B. G. 1963. Certain palaeoniscoid fishes and the evolution of the snout in actinopterygians. *Bull. Br. Mus. nat. Hist.* (Geol.), London, **8**: 255–325, 2 pls., 20 figs.

—— 1970. Osteichthyes. In *McGraw-Hill Yearbook of Science and Technology*, ed. Lapedes: 284–286, 1 fig. McGraw-Hill, New York.

GARSTANG, W. 1931. The phyletic classification of the Teleostei. *Proc. Leeds phil. lit. Soc.* **2**, (5): 240–260.

GAUDANT, J. 1968. Contribution à une révision des *Anaethalion* de Cérin (Ain). *Bull. Bur. Rech. géol. min. Paris*, (2) **4**: 95–115, 6 figs., 3 pls.

GILL, T. 1893. Families and subfamilies of fishes. *Mem. natn. Acad. Sci.*, Washington, **4**: 125–138.

GOODY, P. C. 1969a. *Sedenhorstia dayi* (Hay), a new elopoid from the Cenomanian of Hajula in the Lebanon. *Am. Mus. Novit.*, New York, **2358**: 1–23, 9 figs.

—— 1969b. The relationships of certain Upper Cretaceous teleosts with special reference to the myctophoids. *Bull. Br. Mus. nat. Hist.* (Geol.), London, *Suppl.*, **7**: 1–255, 102 figs.

GOSLINE, W. A. 1960. Contributions toward a classification of modern isospondylous fishes. *Bull. Br. Mus. nat. Hist.* (Zool.), London, **6**: 325–365, 15 figs.

—— 1961. Some osteological features of modern lower teleostean fishes. *Smithson. misc. Collns.*, Washington, **142**, 3: 1–42, 8 figs.

—— 1965. Teleostean phylogeny. *Copeia*, Washington: 186–194, 1 fig.

—— 1967. Reduction in branchiostegal ray number. *Copeia*, Washington: 237–239, 1 fig.

—— 1969. The morphology and systematic position of the alepocephaloid fishes. *Bull. Br. Mus. nat. Hist.* (Zool.), London, **18**: 183–218, 14 figs.

—— 1971. *Functional morphology and classification of teleostean fishes.* Univ. of Hawaii Press, Honolulu: ix + 208 pp., 29 figs.

GREENWOOD, P. H. 1963. The swimbladder in African Notopteridae (Pisces) and its bearing on the taxonomy of the family. *Bull. Br. Mus. nat. Hist.* (Zool.), London, **5**: 377–412, 5 figs., 4 pls.

—— 1966. The caudal fin skeleton in osteoglossoid fishes. *Ann. Mag. nat. Hist.*, London, (13) **9**: 581–597, 12 figs.

—— 1968. The osteology and relationships of the Denticipitidae, a family of clupeomorph fishes. *Bull. Br. Mus. nat. Hist.* (Zool.), London, **16**: 213–273, 34 figs.

—— 1970a. Skull and swimbladder connections in fishes of the family Megalopidae. *Bull. Br. Mus. nat. Hist.* (Zool.), London, **19**: 119–135, 2 figs., 3 pls.

—— 1970b. On the genus *Lycoptera* and its relationship with the family Hiodontidae (Pisces, Osteoglossomorpha). *Bull. Br. Mus. nat. Hist.* (Zool.), London, **19**: 257–285, 10 figs.

GREENWOOD, P. H., MYERS, G. S., ROSEN, D. E. & WEITZMAN, S. H. 1967. Named main divisions of teleostean fishes. *Proc. biol. Soc. Wash.*, **80** : 227–228.

—— ROSEN, D. E., WEITZMAN, S. H. & MYERS, G. S. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bull. Am. Mus. nat. Hist.*, New York, **131** : 339–456, pls. 21–23, 32 charts.

—— & ROSEN, D. E. 1971. Notes on the structure and relationships of the alepocephaloid fishes. *Am. Mus. Novit.*, New York, **2473** : 1–41, 25 figs.

GREGORY, W. K. 1933. Fish skulls : a study of the evolution of natural mechanisms. *Trans. Am. phil. Soc.*, Philadelphia, **23**, 2 : 75–481, 299 figs.

GÜNTHER, A. C. 1877. Preliminary notes on new fishes collected in Japan during the expedition of H.M.S. *Challenger, Ann. Mag. nat. Hist.*, London, (4) **20** : 433–446.

—— 1887. Report on the deep-sea fishes collected by H.M.S. *Challenger* during the years 1873–1876. *Rep. scient. Results Voy. Challenger*, London, **22** : 1–335, 73 pls.

HARRISSON, C. M. H. 1966. On the first halosaur leptocephalus, from Madeira. *Bull. Br. Mus. nat. Hist.* (Zool.), London, **14** : 441–486, 6 figs., 1 pl.

HAY, O. P. 1903. On a collection of Upper Cretaceous fishes from Mount Lebanon, Syria, with description of four new genera and nineteen new species. *Bull. Am. Mus. nat. Hist.*, New York, **19**, 10 : 395–452, 14 pls.

HILDEBRAND, S. F. 1963. Families Elopidae and Albulidae. *In* Fishes of the Western North Atlantic. *Mem. Sears Fdn. mar. Res.*, New Haven, **1**, 3 : xxi + 630 pp., 132 figs.

HILGENDORF, F. 1877. *Pterothrissus*, eine neve Clupeidengattung. *Leopoldina*, Dresden, **13** : 127–128.

HOLLISTER, G. 1936. Caudal skeleton of Bermuda shallow water fishes. I. Order Isospondyli : Elopidae, Megalopidae, Albulidae, Clupeidae, Dussumieridae, Engraulidae. *Zoologica, N.Y.*, **21** : 257–290, 53 figs.

—— 1939. Young *Megalops cyprinoides* from Batavia, Dutch East Indies, including a study of the caudal skeleton and a comparison with the Atlantic species, *Tarpon atlanticus*. *Zoologica, N.Y.*, **24** : 449–475, 21 figs.

HOLSTVOOGD, C. 1965. The pharyngeal bones and muscles in Teleostei, a taxonomic study. *Proc. K. ned. Akad. Wet.* Amsterdam, **68C** : 209–218, 8 figs., 13 pls.

JESSEN, H. 1968. The gular plate and branchiostegal rays in *Elops*, *Amia* and *Polypterus*. *In* Ørvig, T. (ed.), *Nobel Symposium 4, Current problems of lower vertebrate phylogeny* : 429–438, 3 figs. Stockholm.

—— 1972. Schultergürtel und Pectoralflosse bei Actinopterygien. *Fossils and Strata*, Oslo, **1** : 1–101, pls. 1–25.

JORDAN, D. S. 1923. A classification of fishes, including families and genera as far as known. *Stanford Univ. Publs, Biol. Sci.*, Palo Alto, **3** : 79–243.

—— & EVERMANN, B. W. 1896. The fishes of North and Middle America. *Bull. U.S. natn. Mus.*, Washington, **16** : 1–1018.

LACÉPÈDE, B. G. E. 1803. *Histoire naturelle des Poissons*, **5** (1798–1803) : 803 pp. Paris.

LAUBE, G. C. 1885. Eine Beitrage zur Kenntniss der Fische des böhmischen Turons. *Denkschr. Akad. Wiss. Wien.* **1** : 258–298.

LINNAEUS, K. 1758. *Systema Naturae*, 10th ed. : 824 pp. Stockholm.

—— 1766. *Systema Naturae*, 12th ed. : 1327 pp. Stockholm.

LOOMIS, F. 1900. Die Anatomie und die Verwandtschaft der Ganoid und Knochen Fische aus der Kreide Formation von Kansas. *Palaeontographica*, Stuttgart, **46** : 213–284, pls. 19–27.

MCALLISTER, D. E. 1968. Evolution of branchiostegals and classification of teleostome fishes. *Bull. natn. Mus. Can.*, Ottawa, **221** : xiv + 239 pp., 21 pls.

MCDOWELL, S. *In press*. Order Heteromi. *In* Fishes of the Western North Atlantic. *Mem. Sears Fdn. mar. Res.*, New Haven.

MANTELL, G. A. 1822. *The fossils of the South Downs ; or Illustrations of the Geology of Sussex* : 320 pp., 42 pls. Lupton Relfe, London.

MANTELL, G. A. 1838. *The Wonders of Geology* : xvi + 828 pp. Relfe & Fletcher, London.

von der MARCK, W. 1858. Ueber einige Wirbelthiere, Kruster und Cephalopoden der Westphälischen Kreide. *Z. dt. geol. Ges.*, Berlin, **10** : 231–271.

—— 1863. Fossile Fische, Krebse und Pflanzen aus dem Plattenkalk der Jüngsten Kreide in Westphalen. *Palaeontographica*, Cassel, **11** : 1–83, 14 pls.

—— 1868. Neue Fische und Krebse und Pflanzen aus dem Plattenkalk der Jüngsten Kreide in Westphalen. *Palaeontographica*, Cassel, **15** : 269–305, 4 pls.

—— 1873. Neue beitrage zur Kenntniss der fossilen Fische und anderer Thierreste aus der Jüngsten Kreide Westfalens. *Palaeontographica*, Cassel, **22** : 55–74, 2 pls.

—— 1885. Fische der Oberen Kreide Westfalens. *Palaeontographica*, Cassel, **31** : 233–267, 5 pls.

MONOD, T. 1967. Le complexe urophore des Téléostéens : typologie et évolution (note préliminaire). *Colloques int. Cent. natn. Res. scient.*, Paris, **163** : 111–131, 16 figs.

—— 1968. Le complexe urophore des poissons téléostéens. *Mém. Inst. Fond. Afr. noire*, Dakar, **81** : 1–705, 989 figs.

MUNSTER, G. 1842a. Beitrag zur Kenntniss einiger neuen seltenen Versteinerungen aus den lithographischen Sheifern in Baiern. *Neues Jb. Miner. Geogn. Geol. Petrefakt.*, Stuttgart : 35–46.

—— 1842b. Beschreibung einiger neuen Fische aus den lithographischen Scheifern von Bayern. *Beiträge zur Petrefactenkunde*, Bayreuth, **5** : 55–64, 4 pls.

NELSON, G. J. 1967. Gill arches of teleostean fishes of the family Clupeidae. *Copeia*, Washington : 389–399, 9 figs.

—— 1968a. Gill arches of teleostean fishes of the division Osteoglossomorpha. *J. Linn. Soc.* (*Zool.*), London, **47** : 261–277, 11 figs.

—— 1968b. Gill arch structure in *Acanthodes*. *In* Ørvig, T. (ed.), *Nobel Symposium* 4, *Current problems of lower vertebrate phylogeny* : 129–143, 6 figs. Stockholm.

—— 1969a. Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. *Bull. Am. Mus. nat. Hist.*, New York, **141** : 475–552, 26 figs., 13 pls.

—— 1969b. Infraorbital bones and their bearing on the phylogeny and geography of osteoglossomorph fishes. *Am. Mus. Novit.*, New York, **2394** : 1–37, 22 figs.

NORMAN, J. R. 1960. *A draft Synopsis of the Orders, Families and Genera of Recent Fishes and Fish-like Vertebrates* : 1–649. Br. Mus. (Nat. Hist.), London.

NURSALL, J. R. 1964. The jaws of pycnodonts (Holostei : Pycnodontiformes), *Am. Zool.*, New York, **4** : 75.

NYBELIN, O. 1956. Les canaux sensoriels du museau chez *Elops saurus*. *Ark. Zool.*, Stockholm, (2) **10**, 9 : 453–458, 3 figs.

—— 1960. A gular plate in *Albula vulpes* (L.). *Nature, Lond.* **188** : 78.

—— 1963. Zur Morphologie und Terminologie des Schwanzskelettes der Actinopterygier. *Ark. Zool.*, Stockholm, (2) **15** : 485–516, 22 figs.

—— 1964. Versuch einer taxonomischen Revision der jurassischen Fisch-gattung *Thrissops* Agassiz. *Göteborgs K. Vetensk.- o. Vitterh.-Samh. Handl.*, (B) **9** : 1–44, 9 pls.

—— 1967a. Notes on the reduction of the sensory canal system and of the canal-bearing bones in the snout of higher actinopterygian fishes. *Ark. Zool.*, Stockholm, (2) **19** : 235–246, 4 figs.

—— 1967b. Versuch einer taxonomischen Revision der *Anaethalion*-Arten des Weissjura Deutschlands. *Acta R. Soc. scient. litt. gothoburg.*, **2** : 1–53, 5 figs., 1 table, 8 pls.

—— 1968. The dentition in the mouth cavity of *Elops*. *In* Ørvig, T. (ed.), *Nobel Symposium* 4, *Current problems of lower vertebrate phylogeny* : 439–443, 3 figs. Stockholm.

—— 1971. On the caudal skeleton in *Elops* with remarks on other teleostean fiishes. *Acta R. Soc. scient. litt. gothoburg*, **7** : 1–52, 12 pls.

OKADA, Y. 1960. Freshwater fishes of Japan. *J. Fac. Fish. pref. Univ. Mie-Tsu*, **4** (2) : 267–588, 68 figs., 53 pls., 89 tables.

OWEN, R. 1840. *Odontography*, London, 1840–1845 : lxxiv + 655 pp., 168 pls.

—— 1854. *Descriptive Catalogue of the Fossil Organic Remains of Reptilia and Pisces contained in the Museum of the Royal College of Surgeons of England* : xix + 184 pp. London.

PATTERSON, C. 1967a. Are the teleosts a polyphyletic group? *Colloques int. Cent. natn. Res. scient.*, Paris, **163** : 93–109, 11 figs.

—— 1967b. Teleostei. In Harland, W. B. *et al.*, *The Fossil Record* : 654–666. Geological Society, London.

—— 1967c. A second specimen of the Cretaceous teleost *Protobrama* and the relationships of the sub-order Tselfatioidei. *Ark. Zool.*, Stockholm, (2) **19**, 8 : 215–234, 8 figs.

—— 1968a. The caudal skeleton in Lower Liassic pholidophorid fishes. *Bull. Br. Mus. nat. Hist.* (Geol.), London, **16** : 201–239, 5 pls., 12 figs.

—— 1968b. The caudal skeleton in Mesozoic acanthopterygian fishes. *Bull. Br. Mus. nat. Hist.* (Geol.), London, **17**, 2 : 47–102, 28 figs.

—— 1970a. A clupeomorph fish from the Gault (Lower Cretaceous). *J. Linn. Soc.* (*Zool.*), London, **49** : 161–182, 5 figs., 1 pl.

—— 1970b. Two Upper Cretaceous salmoniform fishes from the Lebanon. *Bull. Br. Mus. nat. Hist.* (Geol.), London, **19** : 205–296, 48 figs., 5 pls.

PICTET, F. J. 1850. *Description de quelques poissons fossiles du Mont Liban*, 59 pp., 10 pls. J.-G. Fick, Genève.

—— & HUMBERT, A. 1866. *Nouvelles recherches sur les poissons fossiles du Mont Liban*, vii + 114 pp., 19 pls. Georg, Genève.

POLL, M. 1953. Poissons III. Téléostéens malacoptérygiens. *Rés. sci. expéd. océanogr. Belg. eaux côt. Afr. atlant. sud.* (*1948–1949*), **4**, 2 : 1–258, 8 pls., 104 figs.

PRIEM, F. 1908. Études des poissons fossiles du Bassin Parisien. *Annls Paléont.*, Paris, **3** : 1–144, 5 pls., 74 figs.

REGAN, C. T. 1909. A revision of the fishes of the genus *Elops*. *Ann. Mag. nat. Hist.*, London, (8) **3** : 37–40.

—— 1910. The caudal fin of the Elopidae and some other teleostean fishes. *Ann. Mag. nat. Hist.*, London, (8) **5** : 354–358, 2 figs.

RIDEWOOD, W. G. 1904. On the cranial osteology of the fishes of the families Elopidae and Albulidae, with remarks on the morphology of the skull in the lower teleostean fishes generally. *Proc. Zool. Soc. Lond.*, **2** : 35–81, 18 figs.

ROMER, A. S. 1966. *Vertebrate Palaeontology*, 3rd ed. : viii : 468 pp., 443 figs., 4 tables. Chicago University Press.

ROSEN, D. E. & GREENWOOD, P. H. 1970. Origin of the Weberian apparatus and relationship of the ostariophysan and gonorynchiform fishes. *Am. Mus. Novit.*, New York, **2428** : 1–25, 16 figs.

—— & PATTERSON, C. 1969. The structure and relationships of the paracanthopterygian fishes. *Bull. Am. Mus. nat. Hist.*, New York, **141** : 357–474, 74 figs., pls. 52–78, 8 tables.

SAINT-SEINE, P. de. 1949. Les poissons des Calcaires lithographiques de Cerin (Ain). *Nouv. Archs Mus. Hist. nat. Lyon*, **2** : vii + 357 pp., 26 pls.

SAUVAGE, H. E. 1891. Note sur quelque poissons fossiles du Lias supérieur de l'Yonne. *Bull. Soc. Sci. hist. nat. Yonne*, Auxerre, **45** (2) : 31–45, 3 pls.

—— 1903. Noticia sobre los Peces de la Caliza litográfica de la Provincia de Lérida (Cataluña). *Mems R. Acad. Cienc. Artes Barcelona*, **3** (4), no. 35 : 1–32, 4 pls.

SCOPOLI, G. A. 1777. *Introductio ad historiam naturalem sistema genera lapidum, plantarum et animulium* : 6 + 506 + 34 pp. Prague.

SIEGFRIED, P. 1954. Die Fisch-Fauna des Westfälischen Ober-Senons. *Palaeontographica*, Stuttgart, (A) **106** : 1–36, 15 pls., 2 figs.

STARKS, E. C. 1930. The primary shoulder girdle of the bony fishes. *Stanford Univ. Publs, Biol. Sci.*, Palo Alto, **6** : 3–93, 38 figs.

STEWART, A. 1898. A contribution to the knowledge of the ichthyic fauna of the Kansas Cretaceous. *Kans. Univ. Q.*, Lawrence, **7** : 21–29, 2 pls.

TAYLOR, W. R. 1967. An enzyme method of clearing and staining small vertebrates. *Proc. U.S. natn. Mus.*, Washington, **122** : 1–17.

TCHERNAVIN, V. 1953. *The Feeding Mechanisms of a Deep Sea Fish, Chauliodus sloani Schneider* : 99 pp., 10 pls., 36 figs. Br. Mus. (Nat. Hist.), London.

VETTER, B. 1878. Untersuchungen zur vergleichenden Anatomie der Kiemen- und Kiefermusculatur der Fische. *Jena Z. Naturw.*, **12** : 431–450, 3 pls.

VRBA, E. S. 1968. Contributions to the functional morphology of fishes. Part V. The feeding mechanisms of *Elops saurus* Linnaeus. *Zoologica Afr.*, Cape Town, **3** : 211–236, 9 figs.

WAGNER, A. 1863. Monographie der fossilen Fische aus den lithographischen Schiefern Bayerns. Zweite Abtheilung. *Abh. bayer. Akad. Wiss.*, München, **9** : 611–748, 6 pls.

WENZ, S. 1965. Les poissons Albiens de Vallentigny (Aube). *Annls Paléont.*, Paris, **51** : 1–24, 5 figs., 2 pls.

WHITE, E. I. 1938. The generic name *Aethalion*. *Ann. Mag. nat. Hist.*, London, (10) **19** : 319.

—— 1960. *British Caenozoic Fossils*, 2nd ed. : i–vii + 132 pp., 44 pls. Brit. Mus. (Nat. Hist.), London.

—— & FROST, G. A. 1931. *The Vertebrate Faunas of the English Eocene.* Vol. 1. *From the Thanet Sands to the Basement Bed of the London Clay* : 1–123, 1 pl. Brit. Mus. (Nat. Hist.), London.

—— & MOY-THOMAS, J. A. 1940. Notes on the nomenclature of fossil fishes—Part III, Homonyms M–Z. *Ann. Mag. nat. Hist.*, London, (2) **7** : 395–400.

WHITEHEAD, P. J. P. 1962. The species of *Elops* (Pisces : Elopidae). *Ann. Mag. nat. Hist.*, London, (13) **5** : 321–329, 3 figs.

—— 1963. A contribution towards the classification of clupeoid fishes. *Ann. Mag. nat. Hist.*, London, (13) **5** : 737–750, 3 figs.

WINKLER, T. C. 1862. Description de quelques nouvelles espèces des poissons fossiles du calcaire lithographique de Solenhofen. *Natuurk. Verh. holland Maatsch. Wet. Haarlem*, **16** : 94 pp., 10 pls.

WOODWARD, A. A. & SHERBORN, C. D. 1890. *A Catalogue of British Fossil Vertebrata* : xxxv + 396 pp. Dulau & Co., London.

WOODWARD, A. S. 1888. A synopsis of the vertebrate fossils of the English Chalk. *Proc. Geol. Ass.*, London, **10** : 273–338, 1 pl.

—— 1891. Notes of some fish remains from the Lower Tertiary and Upper Cretaceous of Belgium, collected by Monsieur A. Houzeau de Lehaie. *Geol. Mag.*, London, **8** : 104–114, 1 pl.

—— 1893. Description of the skull of *Pisodus owenii*, an *Albula*-like fish of the Eocene period. *Ann. Mag. nat. Hist.*, London (6) **11** : 357–359, 1 pl.

—— 1895. *Catalogue of the Fossil Fishes in the British Museum* (*Natural History*) : **3** : xlii + 544 pp., 18 pls., 45 figs. Brit. Mus. (Nat. Hist.), London.

—— 1900. On a new specimen of the clupeoid fish *Aulolepis typus* from the English Chalk. *Ann. Mag. nat. Hist.*, London, (7) **5** : 324–326, 1 pl.

—— 1901. *Catalogue of the Fossil Fishes in the British Museum* (*Natural History*), **4**, xxxviii + 636 pp., 19 pls., 22 figs. Brit. Mus. (Nat. Hist.), London.

—— 1907. The fossil fishes of the English Chalk, pt. 3. *Palaeontogr. Soc.* (*Monogr.*), London : 97–128, 6 pls., 14 figs.

—— 1908. The fossil fishes of the English Chalk, pt. 4. *Palaeontogr. Soc.* (*Monogr.*), London : 129–152, 5 pls., 6 figs.

—— 1919. The fossil fishes of the English Wealden and Purbeck Formations, Pt. 3. *Palaeontogr. Soc.* (*Monogr.*), London : 105–148, 6 pls., 6 figs.

—— 1942. Some new and little known Upper Cretaceous fishes from Mount Lebanon. *Ann. Mag. nat. Hist.*, London, (11) **9** : 537–568, 4 figs., 5 pls.

YABE, H. & OKADA, T. 1930. On some fossil fishes from the Cretaceous of Japan. *Jap. J. Geol. Geogr.*, Tokyo, **8** : 1–7, 2 pls.

VIII. ABBREVIATIONS USED IN TEXT-FIGURES

ace	anterior ceratohyal
ao	antorbital
ao.s.c	antorbital sensory canal
apal	autopalatine
a.p.b	anterior opening for periotic bulla
a.ros	anterior rostral ossicle
art	articular
asp	autosphenotic
atfc	anterior opening of pars jugularis
bh	basihyal
boc	basioccipital
brr	branchiostegal ray
bsp	basisphenoid
cb	ceratobranchial (numbered 1-5)
cl	cleithrum
cor	coracoid
c.sc	caudal scute
cy	scale
de	dermethmoid
den	dentary
df	dilatator fossa
dhh	dorsal hypohyal
d.l	dorsal (epiotic) limb of post-temporal
dpal	dermopalatine
dsp	dermosphenotic
eart	endosteal articular
eb 1	first epibranchial
e.com	ethmoid commissure
ecp	ectopterygoid
enp	endopterygoid
ep	epural (numbered 1-3)
epo	epiotic
epo.pr	epiotic process
exo	exoccipital
f.ah	foramen for afferent hyoidean artery
fahm	facet for articulation with hyomandibular
fa.mx	facet for articulation with maxilla
fa.pal	facet for articulation with palatine
fa.pmx	facet for articulation with premaxilla
f.bv	foramen for a blood vessel
fep	foramen for efferent pseudobranchial artery
fhv	foramen for head vein
fica	foramen for internal carotid artery
fm	foramen magnum
foa	foramen for orbital artery
f.ptf	foramen leading to post-temporal fossa
fr	frontal
fsp	foramen for occipital nerve
fuv	fused vertebral centrum
gr.ah	groove for afferent hyoidean artery
gr.V & VII	groove for superficial ophthalmic branches of V & VII
gr.so.s.c	groove for supraorbital sensory canal
gu	gular plate
h	hypural (numbered 1-7)
hb	hypobranchial (numbered 1-3)
hm	hyomandibular
ib	infrapharyngobranchial (numbered 1-3)
ic	intercalar
in	interhyal
io	infraorbital (numbered 1-5)
iop	interoperculum
io.s.c	infraorbital sensory canal
l.e	lateral ethmoid
l.l	lateral line
m.c	Meckelian cartilage
m.cor	mesocoracoid
mes	mesethmoid
mpt	metapterygoid
m.ros	middle rostral ossicle
m.s.c	mandibular sensory canal
mx	maxilla
myp	posterior myodome
na	nasal
np	notochordal pit
npu 1	neural arch associated with first preural centrum
nsp pu	neural spine associated with preural centrum (numbered 2-4)
nu 1	neural arch associated with first ural centrum
op	operculum
ors	orbitosphenoid
ot.s.c	otic sensory canal
pa	parietal
pap	parapophysis
par	parasphenoid
pce	posterior ceratohyal
pcl	postcleithrum (numbered 1-3)
ph	parhypural

pmx	premaxilla
pop	preoperculum
pop.s.c	preopercular sensory canal
p.p.b	posterior opening of periotic bulla
pr.l.e	lateral ethmoid process of autopalatine
pr.mes	mesethmoid process of autopalatine
pro	prootic
pro.ic	prootic-intercalar bridge
p.ros	posterior rostral ossicle
psp	pterosphenoid
ptf	post-temporal fossa
ptfc	posterior opening of pars jugularis
pto	pterotic
ptt	post-temporal
pu	preural centrum (numbered 1–6)
qu	quadrate
r.d	distal radial
ros	rostral ossicles
r.p	proximal radial (numbered 1–4)
sb 1	first suprapharyngobranchial
sca	scapula
scaf	scapular foramen
scl	supracleithrum
sef	sub-epiotic fossa
ses	sesamoid articular
smx	supramaxilla (numbered 1–2)
so	supraorbital
soc	supraoccipital
sop	suboperculum
so.s.c	supraorbital sensory canal
stt	supratemporal
stt.com	supratemporal commissure
suf	subtemporal fossa
sy	symplectic
Tpbb	tooth plate on basibranchial (numbered 1–4)
Tpbh	tooth plate on basihyal
Tpce	tooth plate on ceratohyal
Tpib4	tooth plate on infrapharyngobranchial 4
u	ural centrum (numbered 1–2)
ud	urodermal
un	uroneural (numbered 1–7)
vhh	ventral hypohyal
v.l	ventral (intercalar) limb of post-temporal
vo	vomer
I	foramen for olfactory tract
II	foramen for optic tract
III	foramen for oculomotor
V pal	foramen for palatine ramus of trigeminal
VII hm	foramen for hyomandibular trunk of facial
VII m	foramen for mandibular ramus of facial
VII ot	foramen for otic branch of facial
IX	foramen for glossopharyngeal
X	foramen for vagus

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ORDOVICIAN BRACHIOPODA FROM THE SHELVE DISTRICT, SHROPSHIRE

A. WILLIAMS

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BY
ALWYN WILLIAMS
The University of Birmingham

Pp. 1–163 ; 28 *Plates* ; 11 *Text-figures* ; 110 *Tables*

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ORDOVICIAN BRACHIOPODA FROM THE SHELVE DISTRICT, SHROPSHIRE

By ALWYN WILLIAMS

CONTENTS

SYNOPSIS

A study of fossil Brachiopoda collected mainly as moulds from the Ordovician successions of the Shelve area, reveals the presence of 83 species and subspecies (35 of them new) belonging to 63 genera, of which *Astraborthis*, *Protoskenidioides*, *Salacorthis* and *Whittardia* are new orthaceans, *Caeroplecia* a new triplesiacean, *Eocramatia* a new plectambonitacean and *Bystromena* a new strophomenacean. *Whittardia* is placed in a new subfamily Whittardiinae and *Eocramatia* in a new family Eocramatiidae.

The number of taxa identified in assemblages recovered from any one formation is small, and only exceeds 20 in the Spy Wood Grit and Whittery Shales. This relative poverty of the faunas is at least partly related to rock type, with a dominantly inarticulate association comprising only a few genera prevalent in shales, and a richer, mainly articulate association more typical of the siltstones and sandstones. Both associations evolved by significant replacements of genera as well as species from one horizon to another, so that no combination of taxa can be described as consistently characteristic of either.

The faunas are also restricted in geographical distribution. They show affinities with assemblages from Wales and E. Shropshire and confirm the currently adopted correlation of the

Shelve rocks with the standard Anglo-Welsh succession. However, taxa which also occur in Bohemia and Morocco generally appear earlier in the Shropshire successions and do not assist in precise correlation with either region.

I. INTRODUCTION

THIS paper is primarily a systematic study of Ordovician brachiopods collected by the late Professor W. F. Whittard with the assistance of Mr T. R. Fry during an investigation of the rocks of W. Shropshire that lasted for more than 30 years. Over that period, he amassed an unprecedented number of brachiopods, trilobites, graptolites and miscellaneous invertebrates. The brachiopod collection alone, which is mainly composed of moulds, includes over 3000 specimens well enough preserved to provide statistical information and about half as many identifiable, albeit incomplete, impressions. In fact the collection is not only a tribute to the patience, acute observation and indefatigable energies of Professor Whittard and his assistants, but also a measure of his brilliance as a systematist. Thus when the specimens, all clearly numbered, arrived in the Queen's University of Belfast in 1962, they were so unambiguously documented in relation to his field maps that after his untimely death in 1966 only a few score could not be precisely assigned to a locality, although the stratigraphic horizon of each was accurately known. Almost invariably, therefore, it has been possible to supplement Whittard's original directions and measurements (given in yards) for the identification of fossiliferous localities by citing National Grid references, which indicate position within the kilometre squares of the Ordnance Survey maps. Indeed only two unlocated specimens have been described and figured in the present systematic account, and although this has been done because the specimens are unique, they have not been made the types of any new taxa.

The systematic study itself was begun in 1965. But for various reasons it was discontinued until recently, when it became evident that such a protracted delay in publication of a description of the collection was gravely detrimental to our understanding of British Ordovician palaeogeography and hence of subduction zones of ancient continental plates. In a regional context, the work may be regarded as a supplement to Whittard's own scholarly monographs on the Ordovician trilobites of W. Shropshire. Together with Dr W. T. Dean's forthcoming publication of a geological map of the Shelve area based on Whittard's field studies, and Dr I. Strachan's identification of the graptolitic assemblages, they give a much more comprehensive and detailed assessment of the Ordovician stratigraphy and palaeontology of the Shelve area than ever before.

The collection was given to the writer by Professor Whittard in expectation that it would ultimately find its way to one of the national repositories where it could be adequately housed and curated. Consequently, all specimens, except for a few lost in the preparation of rock sections, have been donated to the Department of Palaeontology of the British Museum (Natural History): their registered numbers, lying in the ranges BB 35305–35600 and BB 37107–37162, are given.

II. FAUNAL DISTRIBUTION

The brachiopods collected from the Ordovician rocks of the Shelve district have been assigned to the 85 identifiable taxa described in the systematic section, with 19 species classified as Inarticulata, 41 as Orthida, 5 as Triplesiida, 15 as Strophomenida, 3 as Pentamerida and 1 each as Rhynchonellida and Spiriferida. The taxa are unevenly distributed in the succession with :

19 species recorded from 36 localities of Mytton Flags (A),
7 „ „ „ 18 „ „ Hope Shales (B),
8 „ „ „ 12 „ „ Stapeley Volcanic Group (C),
5 „ „ „ 16 „ „ Weston Beds (D),
8 „ „ „ 23 „ „ Betton Beds (E),
17 „ „ „ 41 „ „ Meadowtown Beds (F),
16 „ „ „ 52 „ „ Rorrington Beds (G),
21 „ „ „ 8 „ „ Spy Wood Grit (H),
14 „ „ „ 8 „ „ Aldress Shales (I),
15 „ „ „ 4 „ „ Hagley Shales (J),
and 23 „ „ „ 4 „ „ Whittery Shales (K).

In the following comprehensive list of stratigraphic distribution, the lower case letters 'r' (rare), 'fc' (fairly common), 'c' (common), and 'vc' (very common) respectively represent the retrieval of one or more specimens of a listed species in 0–25%, 26–50%, 51–75%, 76–100% of all localities for any one formation, while the capital letters 'A', 'B', 'C' etc. at the head of the list are keys to formations in the order given above. The list is :

	A	B	C	D	E	F	G	H	I	J	K
Apsotreta sp.	r	–	–	–	–	–	–	–	–	–	–
Astraborthis uniplicata gen. et sp. nov.	r	–	–	–	–	–	–	–	–	–	–
Bicuspina modesta sp. nov.	–	–	–	–	–	–	r	c	–	–	–
Bicuspina subquadrata sp. nov.	–	–	–	–	–	–	–	–	r	fc	vc
Bystromena perplexa gen. et sp. nov.	–	–	–	–	–	–	–	vc	–	–	–
Caeroplecia plicata gen. et sp. nov.	–	–	–	–	–	–	–	–	–	r	vc
Conotreta stapeleyensis sp. nov.	–	r	r	–	–	–	–	–	–	–	–
Dalmanella elementaria sp. nov.	r	–	–	–	–	–	–	–	–	–	–
Dalmanella salopiensis sp. nov.	–	–	–	–	r	c	r	–	–	–	–
Dalmanella salopiensis gregaria sp. et subsp. nov.	–	–	–	–	–	–	–	vc	–	–	
Dalmanella salopiensis transversa sp. et subsp. nov.	–	–	–	–	–	–	–	–	fc	–	–
Desmorthis ? sp. nov.	r	–	r	–	–	–	–	–	–	–	–
Diplarelasma sp.	r	–	–	–	–	–	–	–	–	–	–
Dolerorthis cf. *tenuicostata* Williams	–	–	–	–	–	–	–	–	–	–	r
Drabovia cf. *fascicostata* Havlíček	–	–	–	–	–	–	–	fc	–	–	–
Eocramatia dissimulata gen. et sp. nov.	–	r	–	–	–	–	–	–	–	–	–
Euorthisina cf. *moesta minor* Havlíček	r	–	–	–	–	–	–	–	–	–	–
Furcitella sp.	–	–	–	–	–	–	–	–	–	–	r
Gelidorthis cf. *partita* (Barrande)	–	–	–	–	–	–	r	–	–	–	–

	A	B	C	D	E	F	G	H	I	J	K
Glyptorthis viriosa sp. nov.	–	–	–	–	–	r	r	vc	–	–	r
Harknessella cf. *subplicata* Bancroft	–	–	–	–	–	–	–	r	–	–	–
Hesperonomia sp.	r	–	–	–	–	–	–	–	–	–	–
Heterorthis sp.	–	–	–	–	–	–	r	fc	r	–	–
Horderleyella cf. *plicata* Bancroft	–	–	–	–	–	–	–	fc	r	–	–
Horderleyella sp.	–	–	–	–	–	r	–	–	–	–	–
Kiaeromena cf. *kjerulfi* (Holtedahl)	–	–	–	–	–	–	–	–	–	r	r
Kjaerina (*Hedstroemina*) sp.	–	–	–	–	–	–	–	fc	–	–	–
Kullervo sp.	–	–	–	–	–	r	–	–	–	–	–
Lenorthis cf. *proava* (Salter)	fc	–	–	–	–	–	–	–	–	–	–
Leptaena cf. *ventricosa* Williams	–	–	–	–	–	–	–	–	–	fc	c
Lingulella displosa sp. nov.	–	–	–	–	r	r	fc	–	r	–	–
Lingulella displosa petila sp. et subsp. nov.	–	–	fc	–	–	–	–	–	–	–	–
Mcewanella sp.	–	–	–	–	–	–	–	–	–	–	r
Monobolina plumbea (Salter)	c	–	–	–	–	–	–	–	–	–	–
Murinella sp.	–	–	–	–	–	r	–	–	–	–	–
Nicolella cf. *actoniae* (Sowerby)	–	–	–	–	–	–	–	–	–	r	vc
Nocturniella sp.	r	–	–	–	–	–	–	–	–	–	–
Obolus subditivus sp. nov.	–	c	–	–	–	–	–	–	–	–	–
Obolus sp.	r	–	–	–	–	–	–	–	–	–	–
Onniella ostentata lepida subsp. nov.	–	–	–	–	–	–	–	–	fc	vc	vc
Onniella sp.	–	–	–	–	–	–	–	r	–	–	–
Orbiculoidea sp.	–	–	r	–	–	–	–	–	–	–	–
Orthambonites exopunctata sp. nov.	–	–	–	–	–	–	–	–	–	fc	vc
Orthambonites sp.	–	–	–	–	–	–	–	–	r	–	–
Orthis cf. *callactis* Dalman	r	–	–	–	–	–	–	–	–	–	–
Orthis sp.	–	–	r	–	–	–	–	–	–	–	–
Oslogonites ? sp.	r	–	–	–	–	–	–	–	–	–	–
Oxoplecia cf. *nantensis* MacGregor	–	–	–	–	–	r	–	–	–	–	–
Palaeoglossa attenuata (Sowerby)	–	–	–	fc	c	vc	c	c	r	–	r
Palaeoglossa myttonensis sp. nov.	c	–	–	–	–	–	–	–	–	–	–
Palaeostrophomena sp.	–	–	–	–	–	–	–	–	–	–	c
Parastrophinella musculosa sp. nov.	–	–	–	–	–	–	–	fc	–	–	–
Parastrophinella sp.	–	–	–	–	–	–	–	–	–	r	–
Paterula cf. *bohemica* Barrande	r	fc	–	–	r	–	–	–	–	–	–
Paterula cf. *perfecta* Cooper	–	–	–	–	–	r	r	fc	c	–	–
Petrocrania dubia sp. nov.	–	–	–	–	–	–	–	–	r	r	fc
Platystrophia caelata sp. nov.	–	–	–	–	–	–	–	–	–	fc	vc
Platystrophia cf. *major* Williams	–	–	–	–	–	–	–	fc	–	–	–
Plectorthis whitteryensis sp. nov.	–	–	–	–	–	–	–	–	–	r	r
Plectorthis sp.	–	–	–	–	–	–	–	–	r	–	–
Protoskenidioides revelatus gen. et sp. nov.	r	–	–	–	–	–	–	–	–	–	–
Pseudolingula spatula sp. nov.	r	r	–	c	–	fc	r	–	–	–	–
Rafinesquina delicata sp. nov.	–	–	–	–	r	fc	–	–	–	–	–
Rafinesquina sp.	–	–	–	–	–	–	r	–	r	–	r
Reuschella horderleyensis carinata subsp. nov.	–	–	–	–	–	–	–	–	–	c	vc
Rostricellula sparsa Williams	–	–	–	–	–	–	–	r	–	–	–
Salacorthis costellata gen. et sp. nov.	–	–	–	–	–	–	–	fc	–	–	–
Salopia cf. *salteri* (Davidson)	–	–	–	–	–	–	–	r	–	–	–
Salopia sp.	–	–	–	–	–	–	–	–	–	r	fc
Schizocrania salopiensis sp. nov.	–	fc	r	fc	fc	r	c	c	–	–	–
Schizotreta transversa sp. nov.	–	–	–	–	–	r	r	–	–	–	–
Schizotreta sp.	r	r	r	r	–	–	–	–	–	–	–

	A	B	C	D	E	F	G	H	I	J	K
Schmidtites ? simplex sp. nov.	–	–	–	–	r	r	fc	–	fc	–	–
Schmidtites ? simplex subcircularis sp. et subsp. nov.	r	–	fc	–	–	–	–	–	–	–	–
Sericoidea cf. *abdita* Williams	–	–	–	–	–	–	–	–	–	r	–
Skenidioides cf. *costatus* Cooper	–	–	–	–	–	–	r	fc	–	–	c
Sowerbyella cf. *antiqua* Jones	–	–	–	–	–	r	–	–	–	–	–
Sowerbyella multiseptata sp. nov.	–	–	–	–	–	–	–	c	–	–	–
Sowerbyella cf. *sericea permixta* Williams	–	–	–	–	–	–	–	–	fc	–	–
Sowerbyella cf. *sericea* (Sowerby)	–	–	–	–	–	–	–	–	–	fc	vc
Sowerbyella sp.	–	–	–	–	–	–	r	–	–	–	–
Tazzarinia elongata sp. nov.	–	–	–	–	–	r	–	–	–	–	–
Tissintia immatura (Williams)	–	–	–	–	–	fc	–	–	–	–	–
Tissintia prototypa (Williams)	–	–	–	c	fc	–	–	–	–	–	–
Triplesia sp.	–	–	–	–	–	–	–	–	–	–	r
Whittardia paradoxica gen. et sp. nov.	–	–	–	–	–	–	–	–	–	–	c
Zygospira sp.	–	–	–	–	–	–	–	r	–	–	–

The list does not include the few poorly preserved inarticulate brachiopods recovered from the Stiperstone Quartzite which were: a discinid, an obolid and *Pseudolingula* sp.

The large number of identifications reflect the assiduity of the collectors and the great range of geologic time represented by the strata from which specimens have been recovered, rather than any intrinsic richness of faunas. Compared with contemporaneous faunas from Scotland or the Baltic, for example, the Shelve assemblages are restricted in content. This relative paucity may be illustrated (Text-fig. 1) by estimating the number of species recorded per 300 m of rock for each formation, using thicknesses given by Watts (1925) and Whittard (1952). The greatest diversity of about 76 species per 300 m for the Whittery Shales is only one-third that calculated for the penecontemporaneous Balclatchie Mudstones (Williams 1962 : 27). This contrast is further emphasized by the negligible taxonomic communality, even at generic level, between the Shelve assemblages and coeval Scottish or Baltic ones, and appears to be related to profound environmental differences ranking with provincial distinctions (Williams 1973 : 246) in Recent seas. Accordingly only assemblages found in Wales, E. Shropshire and, to a lesser extent, N. Africa and Bohemia are like those of the Shelve area; and even these show discrepancies in stratigraphic distributions and frequencies of occurrence probably linked to the benthic habits of brachiopods.

The brachiopods occurring in the Mytton Flags have an Arenigian aspect even in relation to assemblages characteristic of more remote regions. *Desmorthis*, *Diparelasma* and *Hesperonomia* are reminiscent of American successions (Ulrich & Cooper 1938 : 27–28); *Orthis callactis* (Rubel 1961 : 142) and *Oslogonites* (Öpik 1939 : 118) of the Baltic region; and *Euorthisina* and *Nocturniella* (Havlíček & Vaněk 1966 : 50) of Czechoslovakia, although the species with which the Shelve *Euorthisina* has been compared occurs in the Llanvirnian Šárka Formation of Bohemia and the Llanvirnian Tachilla Shales of Morocco (Havlíček 1971 : 75). With respect to more precise correlation with other Anglo-Welsh successions, only *Lenorthis proava* has

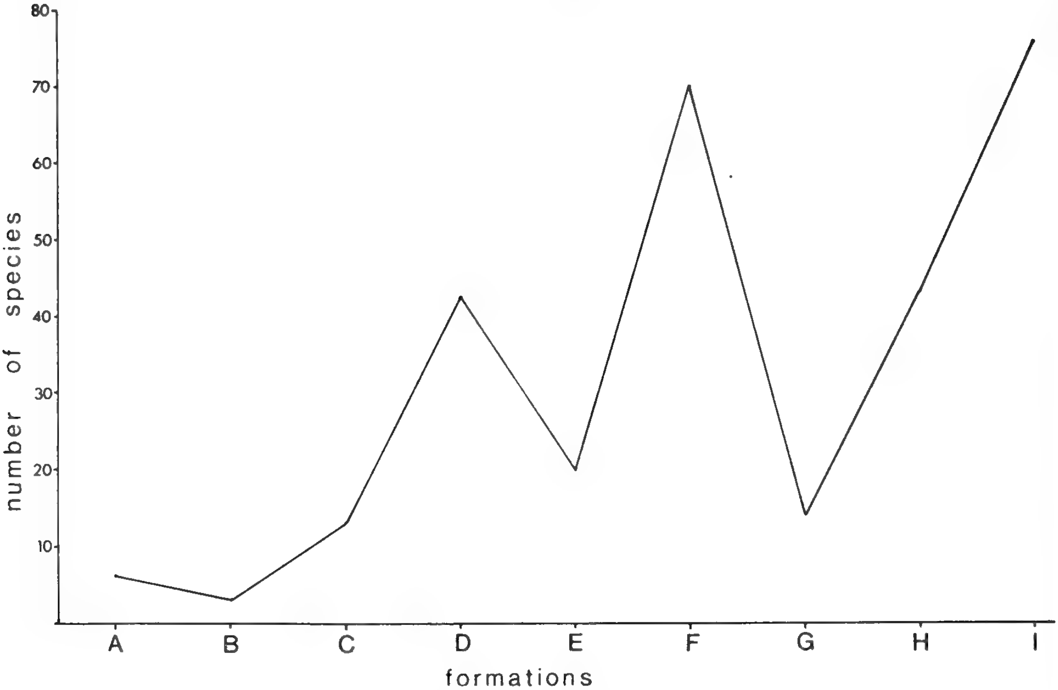


FIG. 1. Graph showing the estimated number of species recorded per 300 m of: Mytton Flags (A); Hope Shales, Stapeley Shales and Weston Beds (B); Betton Beds (C); Meadowtown Beds (D); Rorrington Beds (E); Spy Wood Grit (F); Aldress Shales (G); Hagley Shales (H); and Whittery Shales (I).

proved useful so far. In its type area of Anglesey, this species occurs in Arenigian rocks (Bates 1968 : 147) and is associated with *Hesperonomiella* which is probably closely related to the *Hesperonomia* of the Shelve area. *L. proava* also occurs in the contemporaneous Henllan Ashes of the Arenig district and authenticated reports of its widespread occurrence are in sharp contrast to the lack of information on the distribution of the other common Shelve brachiopod, *Monobolina plumbea*, or of inarticulates generally in the Welsh successions. Clearly these early Ordovician assemblages are in urgent need of investigation.

Despite taxonomic neglect of the older Llanvirn brachiopod faunas, a fairly close likeness between the Llanvirn–Llandeilo assemblages of W. Shropshire and Carmarthenshire can be discerned. This is especially true when one takes into account the longer ranging constituents of the fauna like *Lingulella*, *Palaeoglossa*, *Paterula*, *Pseudolingula* and *Schizocrania* which occur in both areas. However these species, although indicative of similar biofacies, are not very useful for correlation which is dependent on comparatively few articulate species.

Tissintia prototypa is confined to the Weston and Betton formations of the Shelve area, both of which should now be assigned to the Upper Llanvirnian *Didymograptus murchisoni* zone according to I. Strachan (in Whittard 1966 : 297). The species is also narrowly ranging in the Llandeilo area where it occurs in ashy shales of the *Didymograptus bifidus* zone and in the succeeding basal beds of the Ffairfach Grit at Ffairfach. *Tissintia immatura*, on the other hand, is found throughout the Llandeilo Flags (Williams 1953 : 190–194), while its so-called 'variety' *T. immatura plana* is also recorded from conglomeratic sandstones (Williams 1953 : 185) recognized as the top member of the Ffairfach Group–specimens identified as this subspecies, from the basal Ffairfach Grit at Garn-wen, actually belong to *T. prototypa* (Williams 1953 : 184). In the Shelve area, *T. immatura* is restricted to the Meadowtown Beds ; presumably its absence from the Rorrington Beds, which are now correlated with the Middle and Upper Llandeilo Flags (Bassett in Williams *et al.* 1972 : 33), may be attributed to adverse environmental conditions. The distribution of *Tissintia* in Shropshire and Carmarthenshire therefore suggests that the Betton Beds and at least part of the Weston Beds should be correlated with the Ffairfach Group, and the Meadowtown Beds with the Lower Llandeilo and, possibly, the top conglomeratic member of the Ffairfach Group.

Other brachiopods tend to confirm this correlation. *Sowerbyella antiqua* is known from the Betton Beds and from the lower part of the Meadowtown Beds, and although it is common at certain horizons in the Ffairfach Group and Lower Llandeilo, it is unknown from the Middle and Upper Llandeilo Flags. The small *Dalmanella* found in both areas constitute two morphologically distinctive stocks. But the differences between them may have been phenotypic, and it is noteworthy that they first appeared in the Betton and Ffairfach successions simultaneously with *Sowerbyella. Oxoplecia nantensis*, which was first described by MacGregor (1961 : 196) from the Upper Llandeilo rocks of the Berwyn Dome, is widely distributed in the Llandeilo strata of S.W. Wales and a related form has been recovered from the Ffairfach Group. *Horderleyella* on the other hand, which is well represented in Welsh successions, rarely occurs, and then only as an indeterminate species in the Meadowtown Beds. Moreover the Shropshire strophomenid has surprisingly proved to be a new species of *Rafinesquina* unrelated to its well-known contemporary *Macrocoelia llandeiloensis*. This unexpected discovery suggests that the Welsh Llanvirn–Llandeilo strophomenids require revision because those previously identified as the species '*llandeiloensis*' may prove to belong to two different genera.

The graptolite-bearing Rorrington Beds and the trilobite-rich Middle and Upper Llandeilo Flags have different biofacies. Each has yielded a subordinate but distinctive brachiopod assemblage, with a predominance of inarticulates in the Rorrington Beds and of *Tissintia* and *Dalmanella* in the Llandeilo Flags. Indeed articulate brachiopods found in the Rorrington Beds are usually immature specimens indeterminate at infrageneric level, although *Bicuspina*, *Heterorthis* and *Skenidioides*, as precursory elements of the Spy Wood fauna, deserve attention. The first two, together with *Gelidorthis* cf. *partita*, are reminiscent of Middle Caradocian assemblages of Morocco (Havlíček 1971) and Czechoslovakia (Havlíček and Vaněk 1966 : 54–55). This earlier appearance in the Anglo-Welsh successions than in Bohemian or African strata of articulate brachiopods seems to have been part of a recurrent pattern, possibly representing the effects of diachronic migration. Thus *Tissintia* is not known in Morocco until mid-Llandeilo times ; and *Tazzarinia*, which has been collected from

Meadowtown Beds, first occurs in Morocco in the Lower Caradocian part of the Ktaoua Formation.

The greater diversity of post-Rorrington brachiopod faunas affords an opportunity to apply Bancroft's Caradocian stages (1945) to the younger Shelve formations and thereby effect a correlation with the classic sections of E. Shropshire.

The Spy Wood Grit, with *Harknessella* cf. *subplicata*, *Horderleyella* cf. *plicata*, *Salopia* cf. *salteri* and young specimens of *Heterorthis*, may be correlated with the Coston Beds (Dean 1958 : 218). The latter also contain undescribed *Bicuspina*, small *Dalmanella*, *Glyptorthis*, and *Sowerbyella*, which may prove to be conspecific with those found in the Shelve area. Further afield in Wales, the additional presence of *Platystrophia* cf. *major*, *Skenidioides* cf. *costatus* and *Salacorthis* suggests contemporaneity with the early Caradocian faunas of the Arenig district and Anglesey (Whittington and Williams 1955 ; Bates 1968), and W. Carmarthenshire and Pembrokeshire (R. Addison pers. comm.).

The Aldress Shales are less decisively dateable because the pre-Soudleyan brachiopods of E. Shropshire are largely undescribed. But the occurrence of *Sowerbyella* cf. *sericea permixta* is an indirect link through its first appearance within the Nant Hir Mudstones of the Bala district (Bassett, Whittington & Williams 1966 : 263–264) and suggests that the formation is at least Harnagian in age.

The relative richness of the Hagley and Whittery faunas is in keeping with their identification as part of an evolving *Nicolella* association (Williams 1973 : 242). This association is known to have occupied the Anglo-Welsh Basin sporadically throughout Caradocian times, being prevalent in the Costonian Derfel Limestone and Longvillian Gelli-grin Calcareous Ashes of the Bala district (Williams 1963 : 341) and the Upper Longvillian to Actonian formations inclusive of E. Shropshire (Dean 1958 : 221–224). Consequently the Shelve assemblages appear to be partly an anachronistic blend of earlier and later forms. Thus *Caeroplecia*, *Palaeostrophomena*, *Platystrophia* and *Salopia* are also known from the Derfel Limestone although they are represented by different species, but another distinctive member of the association, *Dolerorthis tenuicostata*, is not. In contrast to these similarities, *Nicolella actoniae* (or a subspecies), *Onniella ostentata* and *Sowerbyella sericea* are known from Longvillian successions in N. Wales and/or E. Shropshire. Finally *Bicuspina* and *Reuschella* are unknown from pre-Soudleyan strata and *Kiaeromena* cf. *kjerulfi* and *Leptaena ventricosa* first appear in the Soudleyan Allt Ddu Mudstones. Indeed, bearing in mind the extraordinary range of *N. actoniae* including its occurrence in the Cautleyan Portrane Limestone (Wright 1964 : 165), and the complex relationship among the Sowerbyellas of N. Wales which are mainly closely related to *S. sericea*, the Hagley and Whittery brachiopod assemblages are most likely to be Soudleyan in age.

Like the older brachiopod assemblages, the Caradocian faunas of Shelve contain very few taxa of use in establishing even a tentative correlation with the biostratigraphic successions of other provinces. Only the Caradocian rocks of Bohemia and Morocco have yielded faunas with an overall similarity, although the majority of common elements again first appear in demonstrably younger rocks than in Shropshire in Bohemia (Havlíček and Vaněk 1966 : 53–57). *Heterorthis*, *Horderleyella*, *Onniella* and *Reuschella*, for example, first occur in the Zahorăny Formation, *Dalmanella* in the Letná Formation and *Bicuspina* and *Drabovia* in the Liběn Formation, which have been dated as Soudleyan, Harnagian and Costonian respectively (Williams in Williams *et al.* 1972 : fig. 2). Moreover, even so characteristic a

Standard Succession		Shelve Succession
CARADOC	Soudleyan	Whittery Shales
		Whittery Volcanic Gp.
		Hagley Shales
		Hagley Volcanic Gp.
	— ? — Harnagian	Aldress Shales
	Costonian	Spy Wood Grit
LLANDEILO	Upper Middle	Rorrington Beds
	Lower	Meadowtown Beds
LLANVIRN	Upper	Betton Beds
		Weston Beds
	Lower	Stapeley Shales
		Stapeley Volcanic Gp.
		Hope Shales
ARENIG		Mytton Flags (s.l.)
		Stiperstones Quartzite

FIG. 2. Classification of the Ordovician rocks of the Shelve area according to the brachiopod faunas.

Bohemian stock as *Drabovia* is represented in the Costonian Spy Wood Grit by *D. fascicostata*, which is known in Czechoslovakia only from the allegedly younger Letná Formation.

In summary then, it appears that although the W. Shropshire assemblages of Ordovician brachiopod species are strongly endemic and not reliable indices for correlation outside the Anglo-Welsh Basin, they do confirm the time-stratigraphic classification of the Shelve succession proposed by Dean (in Whittard 1967 : 317) except for the equation of the Rorrington Beds with the Middle and Upper Llandeilian rather than the basal Caradocian (Text-fig. 2).

III. FAUNAL ASSOCIATIONS

The calculation of density distributions of species solely according to the frequency of their presence in localities for any given formation, as in the preceding section, is effective enough for determining the degree to which a taxon is diagnostic of a particular stratigraphic horizon. Such estimates, however, do not give any indication of the relative commonness of occurrence of species recovered from any single locality : of how, for example, *Palaeoglossa myttonensis* and *Protoskenidioides revelata* are recorded from 13 and 3 localities of Mytton Flags respectively, although the former species is represented in the collection by only 16 pedicle or brachial valves compared with 25 valves of the latter. Such data may be very important. They may reflect differences in the transporting capacity of sea currents. Alternatively, the *Palaeoglossa* populations may have consisted of thinly spread individuals tolerant of widely differing environments whereas *Protoskenidioides* may have existed as high density clusters of shells in rigorously circumscribed ecological niches.

Different kinds of data are required to promote investigations into the palaeoenvironment on the one hand and palaeoecosystems on the other. Palaeoenvironmental studies require information on the number of each kind of valve as well as the proportion of complete to fragmented shells composing collections. This demand is well served by data prepared in the manner adopted by Temple (1968 : 9 ; 1970 : 8) for Lower Llandovery brachiopods. Yet for this approach, information on the size range frequencies of species is equally important ; and since such details cannot be derived from normal statistical tables, they are rarely available and the exercise correspondingly diminished in its efficacy. In contrast, studies of relationships within and between communities mainly require estimates of species distribution among communities ; frequencies of individuals representing a species within an association only indicate its importance according to numerical ranking. Nevertheless, such data are valuable from both palaeoecologic and stratigraphic viewpoints. Variation in the numbers of individuals present in fossil communities or their residues may be aids in determining the optimum conditions for the maintenance of a species in space, or in identifying changes in the interrelationship between species of an evolving association in time. In his study of the Shelve trilobites, Whittard (1966 : 298) illustrated variation in the number of specimens collected from each formation by time-histograms. Brachiopods pose a different problem because

TABLE 1

The number of pedicle or brachial valves of the listed species recovered from 22 localities of Mytton Flags

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Apsotreta sp.	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–
Astraborthis uniplicata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
Dalmanella elementaria	–	–	–	–	–	–	–	–	13	1	–	–	–	–	1	–	–	–	–	–	2	3
Desmorthis ? sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Diplarelasma sp.	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–
Euorthisina cf. *moesta minor*	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	2	–	–	2	1	–
Hesperonomia sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Lenorthis cf. *proava*	–	–	7	1	1	–	–	–	7	5	2	1	–	–	–	1	–	3	1	–	2	11
Monobolina plumbea	6	3	1	1	2	2	3	1	–	1	7	–	1	1	5	1	11	2	2	–	–	1
Nocturniella sp.	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Obolus sp.	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–
Orthis cf. *callactis*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	2	1	–
Oslogonites ? sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
Palaeoglossa myttonensis	1	1	1	1	–	1	2	1	1	1	1	–	–	–	2	–	1	1	–	–	–	–
Paterula cf. *bohemica*	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Protoskenidioides revelata	–	–	–	–	–	–	–	–	16	–	–	–	–	–	–	–	–	–	–	–	4	5
Pseudolingula spatula	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Schizotreta sp.	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Schmidtites ? *simplex subcircularis*	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–

each individual is, initially at least, represented in a death assemblage by two valves so that counts of all specimens in collections consisting mainly of disarticulated valves could be a gross misrepresentation of frequencies *in vivo*. Consequently the number of individuals of listed species collected from each locality, shown in Tables 1 to 11, are the totals of the more commonly occurring valves whether they are brachial or pedicle. Also, the tables do not include localities yielding specimens of only one species on the grounds that their distribution does not contribute to our understanding of the relationship within brachiopod associations. Such data may, however, assist in identifying those species most tolerant of palaeoenvironmental variation and have, therefore, been referred to in the explanatory text when this possibility appears to hold.

Table 1 shows the frequency distributions of various brachiopod species collected from 22 localities of Mytton Flags. The fauna was dominated by an association including *Monobolina, Palaeoglossa* and *Lenorthis* (each also occurring alone in 5, 5 and 2 localities respectively) which was especially prevalent in unlaminated micaceous siltstones and fine-grained crystal tuffs. Another association of *Dalmanella, Protoskenidioides* and *Euorthisina* was characteristic of laminated siltstones and shales. The *Monobolina* association has a few elements in common with an association involving *Obolus, Paterula* and *Pseudolingula* found in the dark grey micaceous Hope Shales (Table 2). A similar lithofacies within the Stapeley Volcanic Group (Table 3) supported another inarticulate association with *Lingulella, Schmidtites* and *Schizocrania,* although *Orthis* and *Desmorthis,* which may have been constituents of an association descended from the Arenig *Dalmanella* one, occur in crystal-lithic tuffs.

TABLE 2

The number of pedicle or brachial valves of the listed species recovered from 7 localities of Hope Shales

	1	2	3	4	5	6	7
Eocramatia dissimulata	1	–	–	1	4	–	–
Obolus subditivus	–	3	1	1	–	6	1
Paterula cf. *bohemica*	1	1	1	–	–	1	2
Pseudolingula spatula	–	1	–	1	–	–	1
Schizocrania salopiensis	–	1	–	–	1	1	–

TABLE 3

The number of pedicle or brachial valves of the listed species recovered from 5 localities of Stapeley Shales

	1	2	3	4	5
Conotreta stapeleyensis	4	–	–	–	–
Desmorthis ? sp.	–	1	–	2	–
Lingulella displosa petila	–	–	1	–	1
Orthis sp.	–	3	–	–	–
Schizocrania salopiensis	–	–	1	1	–
Schizotreta sp.	–	–	–	1	–
Schmidtites ? *simplex subcircularis*	1	–	–	–	1

The succeeding Weston and Betton Beds (Tables 4, 5) consist mainly of laminated siltstones. They sustained an association which had evolved out of the Arenigian *Monobolina* complex and was evidently ancestral to the Meadowtown assemblage. In the Weston Beds, the association is dominated by *Pseudolingula*, *Palaeoglossa* and *Tissintia* with the last occurring on its own in five localities additional to those set out in Table 4. By Betton times, changes in the relative importance of species had taken place so that the association was made up mainly of *Palaeoglossa*, *Tissintia* and *Schizocrania* with each of the last two stocks constituting the only brachiopods found in three extra localities.

TABLE 4

The number of pedicle or brachial valves of the listed species recovered from 10 localities of Weston Beds

	1	2	3	4	5	6	7	8	9	10
Palaeoglossa attenuata	1	1	1	–	–	1	–	–	–	1
Pseudolingula spatula	14	2	1	1	2	1	1	–	1	2
Schizocrania salopiensis	1	–	–	1	3	–	–	–	–	–
Schizotreta ? sp.	–	–	–	–	2	–	–	–	–	–
Tissintia prototypa	14	–	–	–	–	–	1	15	3	4

TABLE 5

The number of pedicle or brachial valves of the listed species recovered from 11 localities of Betton Beds

	1	2	3	4	5	6	7	8	9	10	11
Dalmanella salopiensis	–	–	–	–	–	–	–	–	–	5	–
Lingulella displosa	–	–	–	–	–	1	–	–	–	–	–
Palaeoglossa attenuata	2	1	5	1	1	1	1	–	1	–	1
Paterula cf. *bohemica*	–	–	–	–	–	–	–	–	–	1	–
Rafinesquina delicata	–	–	–	–	–	–	–	–	–	6	–
Schizocrania salopiensis	1	–	–	1	1	–	–	1	1	–	–
Tissintia prototypa	–	1	20	–	–	–	7	2	–	–	5

The Meadowtown Beds (Table 6) are essentially laminated calcareous siltstones or fine-grained sandstones with subordinate calcarenites. This lithofacies was occupied by an association derived from the later Llanvirn ones but incorporating new elements, so that the dominant forms were *Palaeoglossa*, *Dalmanella*, *Rafinesquina*, *Tissintia* and *Pseudolingula*. *Palaeoglossa* was the only brachiopod occurring in nine additional localities. The genus must have been more tolerant of variation in the palaeoenvironment than its contemporaries because it is also the dominant member (with *Schmidtites*) of an inarticulate association, descended from the early Llanvirn communities, which includes *Lingula*, *Paterula* and *Pseudolingula* and is found in rarely occurring medium grey shales and mudstones.

The subordinate association identified in the Meadowtown Beds became overwhelmingly important in the Rorrington lithofacies which consisted of medium to dark grey slightly calcareous shales. The principal community (Table 7) was

TABLE 6

The number of pedicle or brachial valves of the listed species recovered from 30 localities of Meadowtown Beds

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Dalmanella salopiensis	21	3	2	–	1	–	–	6	8	1	4	3	3	1	–	1	–	–	25	2	4	13	114	5	–	1	25	1	1	4
Glyptorthis viriosa	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	3	–	–	–	3	–	–	–
Horderleyella sp.	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Kullervo sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
Lingulella displosa	–	–	–	–	–	–	–	2	–	–	1	–	–	2	1	–	1	–	–	–	–	–	1	–	–	–	–	2	–	–
Murinella sp.	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Oxoplecia cf. *nantensis*	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
Palaeoglossa attenuata	1	2	2	2	2	5	2	1	12	–	2	–	–	6	5	1	11	1	1	–	–	2	2	5	3	–	1	14	–	–
Paterula cf. *bohemica*	–	–	–	–	–	–	1	–	4	–	–	–	–	–	–	–	–	–	6	–	–	1	5	–	–	–	1	–	–	–
Pseudolingula spatula	5	1	–	–	–	–	–	2	–	–	3	2	–	–	–	–	–	1	–	–	1	2	9	1	–	–	5	–	–	–
Rafinesquina delicata	25	3	2	1	–	–	–	4	5	1	7	3	2	–	1	–	–	–	10	2	2	10	48	–	–	–	11	–	1	2
Schizocrania salopiensis	–	–	–	–	–	–	–	1	3	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	1	–	–	–	–	–
Schizotreta transversa	–	–	–	–	–	3	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Schmidtites ? *simplex*	–	–	–	–	–	–	14	–	–	–	–	–	–	–	–	1	2	1	–	–	–	–	–	–	–	–	–	–	–	–
Sowerbyella cf. *antiqua*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	50	–	–	1
Tazzarinia elongata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–
Tissintia immatura	35	2	2	1	–	–	–	4	3	–	6	–	–	–	–	–	1	–	10	–	2	2	48	3	–	–	13	–	–	–

TABLE 7

The number of pedicle or brachial valves of the listed species recovered from 29 localities of Rorrington Beds

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Bicuspina cf. *modesta*	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1
Dalmanella cf. *salopiensis*	–	–	–	1	2	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gelidorthis cf. *partita*	–	–	–	–	–	–	–	–	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Glyptorthis sp.	–	–	–	–	2	–	–	–	1	–	–	–	–	–	4	–	–	–	–	–	–	–	–	2	–	–	–	–	–
Heterorthis sp.	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lingulella displosa	3	–	1	–	–	–	–	–	–	1	2	1	–	–	5	–	–	1	2	2	–	–	–	4	1	–	–	–	–
Palaeoglossa attenuata	10	7	1	–	1	1	2	2	1	3	3	–	1	1	10	2	–	2	6	2	–	2	1	3	1	2	1	–	1
Pseudolingula spatula	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
Rafinesquina sp.	–	–	–	–	1	–	–	–	5	1	1	–	–	–	2	1	–	–	–	–	–	–	1	1	–	–	–	1	–
Schizocrania salopiensis	2	–	–	4	–	10	10	11	2	1	8	6	1	5	11	1	1	–	–	–	2	1	–	2	1	–	1	–	1
Schizotreta transversa	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–
Schmidtites ? *simplex*	4	4	–	–	–	–	–	–	–	–	8	–	–	–	7	4	1	1	–	1	1	1	–	4	2	1	–	2	–
Skenidioides cf. *costatus*	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sowerbyella sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–

composed of *Palaeoglossa, Schmidtites* and *Schizocrania* with the last genus alone occurring in six extra localities and each of the first two in an additional five. Immature shells of *Rafinesquina* are most widely distributed, followed by *Dalmanella* and *Glyptorthis*. These presumably represent unsuccessful waves of colonization by an association akin to those characteristic of the Meadowtown Beds and the succeeding calcareous Spy Wood Grit (Table 8). The Spy Wood community is dominated by articulate brachiopods like *Dalmanella, Glyptorthis, Bystromena, Bicuspina* and *Sowerbyella*, although *Palaeoglossa* and *Schizocrania* persist.

TABLE 8

The number of pedicle or brachial valves of the listed species recovered from 7 localities of Spy Wood Grit

	1	2	3	4	5	6	7
Bicuspina modesta	–	–	4	2	1	50	12
Bystromena perplexa	1	2	2	–	1	8	7
Dalmanella salopiensis gregaria	–	3	7	2	1	76	25
Drabovia cf. *fascicostata*	1	–	1	–	–	12	–
Glyptorthis viriosa	1	–	1	1	1	21	4
Harknessella cf. *subplicata*	–	–	–	–	–	–	1
Heterorthis sp.	–	–	–	–	1	10	2
Horderleyella cf. *plicata*	–	–	–	–	–	3	1
Kjaerina (*Hedstroemina*) sp.	–	–	–	–	–	1	1
Onniella sp.	–	–	–	1	–	–	–
Palaeoglossa attenuata	1	1	–	–	–	18	4
Parastrophinella musculosa	–	–	–	–	–	6	2
Paterula cf. *perfecta*	–	3	–	1	–	4	–
Platystrophia cf. *major*	–	–	–	–	–	1	1
Rostricellula sparsa	–	–	–	–	–	5	–
Salacorthis costellata	–	–	1	–	–	5	2
Salopia cf. *salteri*	–	–	–	–	–	2	–
Schizocrania salopiensis	1	–	–	1	1	13	3
Skenidioides cf. *costatus*	–	–	4	–	–	3	–
Sowerbyella multiseptata	–	1	–	1	–	24	11
Zygospira sp.	–	–	–	–	–	1	–

The Aldress Shales, like many of the older formations, bear traces of two distinct associations (Table 9). The more commonly occurring is typified by *Paterula* and *Schmidtites* which have also been recovered from three and one extra localities respectively, and is found in medium grey micaceous siltstones. Crystal tuffs, on the other hand, supported a relatively prolific fauna dominated by *Sowerbyella, Dalmanella* and *Onniella*.

The fossil-bearing members of the two youngest Ordovician formations preserved in the Shelve area, the Hagley and Whittery Shales, consist mainly of light olive-grey calcareous tuffs and mudstones. However, the Whittery mudstones contain lithic and crystal fragments of volcanic debris up to 1 cm in size, mud balls and broken shells, which suggest that even those parts of the formation not obviously derived from volcanic ash falls may have been deposited by lahars. Indeed the only non-volcanic sediment appears to be a light olive-grey micaceous siltstone

Table 9

The number of pedicle or brachial valves of the listed species recovered from 3 localities of Aldress Shales

	1	2	3
Bicuspina subquadrata	–	–	1
Dalmanella salopiensis transversa	–	1	33
Heterorthis sp.	–	–	1
Horderleyella sp.	–	–	7
Onniella ostentata lepida	–	2	22
Orthambonites sp.	–	–	1
Palaeoglossa attenuata	1	–	–
Paterula cf. *perfecta*	1	–	–
Petrocrania dubia	–	–	1
Platystrophia cf. *major*	–	–	1
Plectorthis sp.	–	–	1
Rafinesquina sp.	–	–	1
Schmidtites ? simplex	1	–	–
Sowerbyella sericea permixta	–	2	66

occurring in the Hagley Shales. This lithofacies bears *Sericoidea*, while the rest of the formation contains an association descended from that occurring in the Aldress tuffs but with *Onniella* and *Reuschella* dominant, *Sowerbyella* playing a subordinate role and *Dalmanella* no longer occurring (Table 10). This fauna attained its full diversity in the Whittery mudstones where *Bicuspina, Caeroplecia, Nicolella, Onniella, Orthambonites, Reuschella* and *Whittardia* are very common (Table 11). Many constituents, including *Caeroplecia, Nicolella, Orthambonites, Palaeostrophomena* and *Platystrophia*, reveal that the fauna is mainly composed of the *Nicolella*

Table 10

The number of pedicle or brachial valves of the listed species recovered from 4 localities of Hagley Shales

	1	2	3	4
Bicuspina subquadrata	–	–	1	1
Caeroplecia plicata	–	–	–	1
Kiaeromena sp.	2	–	–	–
Leptaena cf. *ventricosa*	2	1	–	–
Nicolella cf. *actoniae*	–	–	–	1
Onniella ostentata lepida	4	1	1	3
Orthambonites sp.	1	–	–	1
Parastrophinella sp.	–	–	–	1
Petrocrania dubia	–	–	–	1
Platystrophia caelata	1	–	–	1
Plectorthis whitteryensis	–	–	–	2
Reuschella horderleyensis carinata	1	–	2	1
Salopia sp.	–	–	–	1
Sericoidea cf. *abdita*	–	10	–	–
Sowerbyella cf. *sericea*	2	–	–	2

TABLE II

The number of pedicle or brachial valves of the listed species recovered from 4 localities of Whittery Shales

	1	2	3	4
Bicuspina subquadrata	2	1	17	15
Caeroplecia plicata	3	–	14	7
Dolerorthis cf. *tenuicostata*	–	–	3	–
Furcitella sp.	–	–	1	–
Glyptorthis viriosa	–	–	2	–
Kiaeromena sp.	1	–	–	–
Leptaena cf. *ventricosa*	–	1	1	1
Mcewanella sp.	–	–	–	2
Nicolella actoniae	3	9	6	5
Onniella ostentata lepida	4	3	9	25
Orthambonites exopunctata	4	7	12	11
Palaeoglossa attenuata	1	–	–	–
Palaeostrophomena sp.	1	1	1	–
Petrocrania dubia	–	–	1	3
Platystrophia caelata	1	2	2	2
Plectorthis whitteryensis	–	–	7	2
Rafinesquina sp.	–	–	1	–
Reuschella horderleyensis carinata	12	11	6	3
Salopia sp.	–	–	2	1
Skenidioides cf. *costatus*	1	–	2	1
Sowerbyella cf. *sericea*	2	1	1	8
Triplesia sp.	–	–	–	1
Whittardia paradoxica	3	–	8	2

association (Williams 1973 : 242), but elements like *Bicuspina* and *Leptaena* further suggest that remnants of the *Dinorthis* association may also be present.

In conclusion, it is noteworthy that the composition of brachiopod assemblages collected from the Ordovician succession of Shelve appears to be closely connected with the nature of the entombing sediments. In general, two main groups seem to be involved : an inarticulate association connected with the finer clastic sediment and a predominantly articulate one sustained in the coarser, banded, sporadically calcareous siltstones or fine sandstones. Both associations may be traced throughout much of the Ordovician succession with one dominant over the other. Both show profound changes in the composition and relative importance of their constituent taxa and, thereby, greatly reduce the prospects for precise interprovincial correlation.

IV. SYSTEMATIC METHODS

The procedure adopted during the systematic study of the Shelve brachiopods was to quantify, wherever possible, any morphological variation displayed by conspecific specimens from any one locality or horizon and evaluate differences detected among congeneric samples by standard statistical tests for significance. This method is similar to that used by the writer during researches on Girvan and Bala faunas (Williams 1962 : 69–79 ; 1963 : 333), and requires only a few words of explanation.

The number of individuals attributable to any species represented in the collection is small enough to warrant not only the invariable use of small sample techniques but, for many taxa, nothing more than the mean (or mode) and range of variability. Continuous univariate characters which are assumed to be normally distributed, like the distances at which folds originate anterior of umbones or the wavelengths of ribs at a given distance antero-medially of the umbo, have been compared by the *t*-test. Discontinuous univariate characters, like the number of costae ornamenting valves or the relative branching of costellae enumerated according to Bancroft's notation (Bancroft 1945 : 186 ; Williams 1962 : 77), have been compared by χ^2 tests, or contingency or two-by-two tables dependent on the size of samples.

Continuous variables derived by measuring the shell or its several parts, like the cardinalia, dental plates or muscle impressions, are expressions of incremental proportional growth, which may or may not be allometric, and all show very high positive (or rarely negative) correlations with one another. The significance of any differences in estimates of such parameters has been determined by statistical analysis of a series of bivariate distributions. The method is adequate for the comparison of such closely inter-related estimates of shell growth. It also has the advantage of not obscuring the identity of those characters that underwent changes in the rate of growth during cladogenetic or phylogenetic speciation. The development of significantly longer dental plates in one of a number of compared species, for example, will be apparent whether the lengths of plates are consistently paired with the lengths, maximum widths or depths of the pedicle valves in compared samples.

In estimating variation in outline, shape and relative size of the brachiopod skeleton, very many measurements in almost any plane or direction may be taken, provided the same disposition is adopted in measuring all individuals in compared samples. However, certain orientations for the measurement of shells or their impressions have become widely favoured by brachiopod researchers over the years

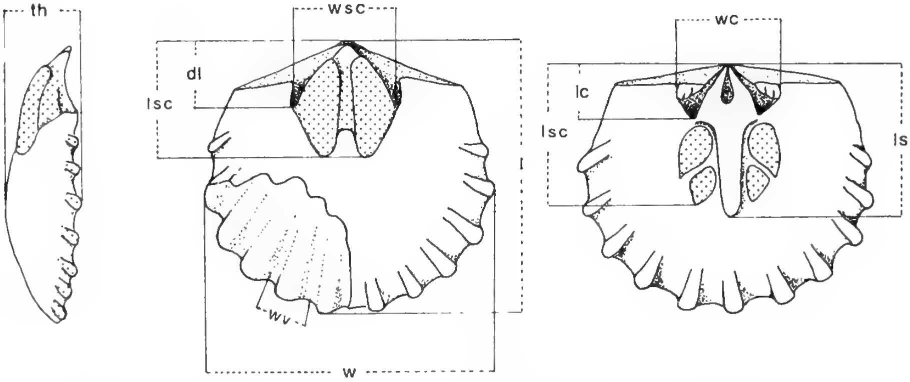


Fig. 3. Diagrammatic representation of moulds (and adherent shell) of *Orthambonites* to show the orientation adopted for measuring certain dimensions including: length (l), maximum width (w) and thickness (th) of a valve, the wavelength of a costa (wv), the length of dental plates (dl), the length (lsc) and width (wsc) of muscle scars, the length of a median ridge (ls), and the length (lc) and width (wc) of brachiophore bases.

and may be regarded as standard. These include length (sagittal), width (maximum) and depth (maximum). Certain orientations for the measurement of internal features are also coming into general use although they have not yet been standardized. Those used in this paper are illustrated in Text-fig. 3, in relation to internal moulds which lend themselves very well to estimating the forward extensions of the bases of dental plates, brachiophores and sockets, or of muscle scars.

V. SYSTEMATIC PALAEONTOLOGY

Class *INARTICULATA* Huxley 1869
Order LINGULIDA Waagen 1885
Superfamily **LINGULACEA** Menke 1828
Family **OBOLIDAE** King 1846
Subfamily **OBOLINAE** King 1846
OBOLUS Eichwald 1829
Obolus subditivus sp. nov.
(Pl. 1, figs. 1–8)

DIAGNOSIS. Biconvex, subcircular *Obolus* almost as long as wide with a lenticular ventral pseudointerarea extending anteriorly for 15% of the length of the pedicle valve and a dorsal pseudointerarea not divided into propareas by an identifiable median groove.

DESCRIPTION. Subcircular, biconvex, *Obolus* with a mean length relative to width of 95% (range 83% to 111%) and a mean depth relative to length of 14% (range 12% to 17%) for 6 pedicle valves, and a brachial valve about one-tenth as deep as long, both valves evenly convex transversely but flattened slightly anteriorly; beaks marginal; shell surface ornamented by concentric growth lines and up to 10 impersistent low narrow plicae.

Striated pseudointerarea of pedicle valve lenticular in outline, orthocline to anacline in attitude, extending forward for 15% of the length of 6 pedicle valves (range 12% to 20%) and divided into 2 propareas by a shallow pedicle groove bearing a fine low median ridge; ventral muscle impressions unknown.

Striated pseudointerarea of brachial valve obtusely triangular, orthocline, extending forward for only one-twentieth of the length of the brachial valve, median groove not identifiable; a pair of elongate muscle scars, possibly representing lateral muscle bases, are vaguely impressed on either side of a low obscure median ridge.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	External and internal moulds of pedicle valve (BB 35573a, b)	5·0	4·6
PARATYPES	External and internal moulds of pedicle valve (BB 35574a, b)	3·3	3·1
	External and internal moulds of brachial valve (BB 35575a, b)	3·8	3·8

Horizon and locality. Hope Shales exposed in path west of Brithdir Farm, 1 mile ENE of Old Church Stoke (Grid Ref. SO 300953).

Discussion. The attribution of relatively small obolids found in the Hope Shales to *Obolus* s.s. is a matter of convenience until more is known about the musculature of the new species, which was not accommodated by well-developed platforms as in more typical species. Even the identification of the species as an obolinid may be a matter of dispute because the dorsal pseudointerarea does not bear an identifiable median groove although it is certainly a better developed feature than the striated thickening of the posterior margin characteristic of the glossellinid brachial valve. In respect of both features, the new species differs from orthodox *Obolus*. However, Cooper (1956 : 189–193) assigned a few species to the genus which bear some resemblance to *O. subditivus*. This is especially true of *O.* ? *biconvexa* Cooper from the Lower Paperville Formation of Tennessee and the closely related *O.* ? *nitens* Cooper from the Lower Rich Valley Formation of Virginia, although both are more elliptically elongate and lack radial plicae, while the former is further distinguished by the presence of concentric undulations.

Obolus sp.

(Pl. 1, figs. 9, 10)

In contrast to *O. subditivus* sp. nov., a few exfoliated valves have been recovered from the Mytton Flags, which are more representative of typical *Obolus*. The exposures in Bergam Quarry above Tankerville Mine (Grid Ref. SO 355995) have yielded an evenly convex pedicle valve (BB 35581a, b) about 6 mm long, which is transversely oval in outline with a length about 70% of the width and a depth 25% of the length. A heart-shaped postero-medial portion of the valve has broken away and probably constitutes the muscle platform. No identifiable impressions are preserved on the internal mould of the platform but a well-defined pedicle groove is seen medially indenting a relatively narrow pseudointerarea.

Another incomplete specimen (BB 35582) about 8 mm wide and over 1 mm deep has been collected from near an adit 290 yds. west of Wood House (Grid Ref. SJ 336002). It bears a pair of submedial muscle scars and may be the brachial valve of the same species. Even so, paucity of material precludes specific identification.

SCHMIDTITES Schuchert & Le Vene 1929

Schmidtites ? ***simplex*** sp. nov.

(Pl. 1, figs. 11–15)

Diagnosis. Subequally biconvex, circular obolids with valves almost as long as wide and 10% as deep as long, ornamented by fila and overlapping lamellae; pseudointerareas narrow, probably striated and divided by relatively wide pedicle groove and median dorsal depression.

Description. Subequally biconvex, circular obolids with inconspicuous beaks and valves 99% as long as wide and 10% as deep as long; ornamented by strong fila, becoming less distinct medially, and finely developed overlapping lamellae ; however the thin shell is usually preserved in a collapsed state commonly expressed as transverse or even radiating wrinkles.

Ventral interior with a narrow crescentic striated pseudointerarea divided by a relatively wide pedicle groove ; muscle impressions known only in one specimen as a pair of suboval, submedial scars, possibly flanked by another set, distinguishable as smooth areas in a finely pitted internal surface.

Dorsal pseudointerarea with a very narrow thickened zone along the posterior margin which may represent a medially grooved pseudointerarea ; other internal features unknown although a low median ridge extends forwards for three-quarters the length of some valves.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	External and internal moulds of pedicle valve (BB 37134a, b)	4·5	4·5
PARATYPES	External and internal moulds of brachial valve (BB 37135a, b)	3·0	2·7
	Exterior of pedicle valve (BB 37136)	3·5	4·0
	External and internal moulds of pedicle valve (BB 37137a, b)	2·6	–
	Internal mould of brachial valve (BB 37138)	4·2	4·5
	Internal mould of pedicle valve (BB 37139)	4·0	–
	External and internal moulds of pedicle valve (BB 37140a, b)	3·5	3·5

HORIZON AND LOCALITIES. Rorrington Beds : BB 37134, 37138 from exposures in Holywell Brook 160 yds WNW of the Mount, Rorrington (Grid Ref. SJ 299007) ; BB 37135, 37139 from outcrops in Deadman's Dingle 100 ft upstream from junction with Spy Wood Brook (Grid Ref. SO 280960) ; BB 37136 from exposures 60 yds north-west of the Mount, Rorrington (Grid Ref. SJ 302005) ; BB 37137, 37140 from the tributary to Lower Wood Brook 340 yds south-east of Desert (Grid Ref. SJ 308017).

Schmidtites* ? *simplex subcircularis sp. et subsp. nov.

(Pl. 1, figs. 16, 17 ; Pl. 2, fig. 1)

DIAGNOSIS. Like *Schmidtites* ? *simplex* but subcircular with valves 96% as wide as long and 7% as deep as long ; protegulum semicircular about 0·2 mm long.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	Exterior of pedicle valve (BB 37141)	2·5	2·8
PARATYPES	External and internal moulds of pedicle valve (BB 37142a, b)	3·0	3·0
	External and internal moulds of brachial valve (BB 37143a, b)	3·3	3·6

Horizon and locality. All specimens from Stapeley Shales exposed in Whitsburn Dingle 650 yds WSW of Lord's Stone, Leagh (Grid Ref. SJ 328019).

Discussion. Subcircular inarticulates, occurring fairly abundantly in the Stapeley Shales and the Meadowtown and Rorrington Beds, are provisionally assigned to the obolid genus *Schmidtites* only because of the lack of muscle platforms which are normally elaborate structures in other obolinids. With regard to the modest differentiation of the posterior margins, here interpreted as poorly developed pseudointerareas, the new species differs even from other described *Schmidtites*, and may eventually prove to be generically separable from all other lingulaceans, to which superfamily it almost certainly belongs.

Notwithstanding the obscurity of internal features and simplicity of shape, the conspecific Meadowtown and Rorrington samples are significantly different ($p < 0·02$) from specimens recovered from the Stapeley Shales which became progressively longer than wide during growth (Table 12). The difference has been recognized by the erection of a new subspecies.

Table 12

Statistics of length (l) and maximum depth (w) of n pedicle valves of *Schmidtites* ? *simplex* sp. nov. from the Rorrington Beds (A) and the Meadowtown Beds (B), and of *Schmidtites* ? *simplex subcircularis* sp. et subsp. nov. from the Stapeley Shales (C)

	A	B	C
n	29	20	9
$\bar{l}$ mm (var l)	2·88 (1·148)	2·98 (1·235)	3·13 (3·23)
$\bar{w}$ mm (var w)	2·9 (1·145)	3·01 (1·244)	3·00 (1·952)
r	0·995	0·977	0·986
$\overline{\log_e l}$ (var $\log_e l$)	0·9927 (0·1296)	1·0288 (0·1296)	0·1 (0·2844)
$\overline{\log_e w}$ (var $\log_e w$)	0·9996 (0·1279)	1·0358 (0·129)	1·0004 (0·1963)
r_e	0·995	0·979	0·99
α (var α)	0·9931 (0·00037)	0·9975 (0·00231)	0·8307 (0·00195)

Subfamily **LINGULELLINAE** Schuchert 1893

LINGULELLA Salter 1866

Lingulella displosa sp. nov.

(Pl. 2, figs. 2–8)

Diagnosis. Ventribiconvex, elongately oval to subtriangular *Lingulella* with a brachial valve 87% as wide as long and a pedicle valve up to 13% as deep as long, ornamented by impersistent concentrically arranged lamellae, pedicle groove and dorsal pseudointerarea extending anteriorly for 9% and 7% to the valve length respectively.

Description. Ventribiconvex *Lingulella* normally changing in outline from elongately oval to subtriangular with a broadly rounded to truncated anterior margin by an acceleration in antero-lateral shell accretion during adult growth stages; brachial valve 87% as wide and less than 10% as deep as long, pedicle valve about 13% as deep as long and 87% as wide as long (range 77% to 97% for 6 specimens), both valves evenly convex in longitudinal and transverse profiles; external surface ornamented by concentrically disposed impersistent lamellae giving a finely scalloped appearance; ventral beak acute, dorsal beak obtusely rounded.

Ventral pseudointerarea striated, slightly anacline to orthocline, crescentic in outline and divided into 2 curved propareas by a shallow, relatively wide pedicle groove extending forward for 9% of the valve length; umbonal muscle scars suboval located immediately anteriorly of the propareas; 2 short, low ridges narrowly diverge from the anterior end of the pedicle groove.

Dorsal pseudointerarea striated, orthocline, lenticular in outline and extending forward for 7% of the length of the brachial valve; dorsal muscle impressions unknown; postero-medial internal surfaces of both valves sporadically and shallowly pitted.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	Incomplete external and internal moulds of pedicle valve (BB 37144a, b)	14·0	11·5
PARATYPES	External and internal moulds of pedicle valve (BB 37146a, b)	12·0	10·0
	External and internal moulds of brachial valve (BB 37147a, b)	15·0	11·0
	External and internal moulds of pedicle valve (BB 37148a, b)	14·0	12·0
	Internal mould of brachial valve (BB 37149)	14·5	14·0

HORIZONS AND LOCALITIES. Meadowtown Beds: BB 37144 from exposures 80 yds from Meadowtown Quarry along the Rorrington road (Grid Ref. SJ 311012); BB 37146 from a small excavation in the corner of a field alongside the cart-track from Meadowtown to Waitchley 330 yds due south of Waitchley (Grid Ref. SJ 311017); BB 37147 from outcrops 570 yds south-west of Meadowtown Quarry (Grid Ref. SJ 306009); BB 37148 from outcrops along the lane to Lower Ridge from bench mark 754, Little Weston (Grid Ref. SO 293984); BB 37149 from Rorrington Beds exposed in Lower Wood Brook 400 ft south-east of the Meadowtown–Rorrington road (Grid Ref. SJ 307008).

Lingulella displosa petila sp. et subsp. nov.

(Pl. 2, figs. 9–11; Pl. 3, fig. 1)

DIAGNOSIS. Gently biconvex, suboval *Lingulella* with a brachial valve 70% as wide as long, ornamented by impersistent concentrically arranged lamellae, pedicle groove and dorsal pseudointerarea extending anteriorly for 13% and 8% of the valve length respectively.

DESCRIPTION. Subequally biconvex *Lingulella* normally suboval in outline with well-rounded anterior margins and a maximum width at about 60% of the shell length anterior of the umbones; pedicle valve about 5% as deep as long and, on average, 70% as wide as long (range 63% to 80% for 5 specimens), both valves gently and evenly convex in longitudinal and transverse profiles ; external surface ornamented by concentrically disposed impersistent lamellae giving a finely scalloped appearance ; ventral beak sharply acute, dorsal beak less conspicuous and more rounded.

Ventral pseudointerarea striated, anacline to orthocline, crescentic in outline and divided into two obliquely disposed propareas by a shallow pedicle groove extending forward for about 13% of the valve length ; ventral muscle impressions unknown.

Dorsal pseudointerarea striated, orthocline, lenticular in outline and extending forward for 5% of the valve length ; dorsal muscle impressions unknown ; fine median ridge faintly developed for over half the valve length, postero-medial internal surfaces of both valves sporadically and shallowly pitted.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	External and internal moulds of pedicle valve (BB 37150a, b)	10·0	6·0
PARATYPES	External and internal moulds of brachial valve (BB 37151a, b)	8·0	6·0
	External and internal moulds of pedicle valve (BB 37152a, b)	–	6·0

TYPE HORIZON AND LOCALITY. All specimens from the Stapeley Volcanic Group exposed in Whitsburn Dingle, 650 yds WSW of Lord's Stone, Leagh (Grid Ref. SJ 328019).

DISCUSSION. Ordovician *Lingulella* from the Shelve area appear to differ from other known *Lingulella* in being ornamented by finely scalloped lamellae. The pattern is reminiscent of *Glyptoglossella* although in other respects, notably the presence of a dorsal pseudointerarea, the specimens cannot even be assigned to the same subfamily. The change in outline from oval to subtriangular that took place during the

TABLE 13

Statististics of length (l) and maximum width (w) of n brachial valves of *Lingulella displosa* sp. nov. from the Rorrington Beds (A) and the Meadowtown Beds (B)

	A	B
n	12	8
l mm (var l)	8·84 (14·383)	8·05 (25·209)
$\bar{w}$ mm (var w)	8·6 (13·647)	6·97 (19·902)
r	0·986	0·97
a (var a)	0·9741 (0·00269)	0·8885 (0·00774)

TABLE 14

Statistics of length (l) and maximum depth (w) of 8 pedicle valves of *Lingulella displosa* sp. nov. from the Rorrington Beds

l mm (var l)	4·76 (8·931)
$\bar{w}$ mm (var w)	4·37 (8·494)
r	0·994
a (var a)	0·9752 (0·00184)

growth of *L. displosa* is also unusual, although a similar acceleration in growth along antero-lateral vectors was responsible for the subtriangular appearance of adult shells of the Tremadocian *L. lingulaeformis* (Mickwitz) from the Baltic area (Goryanski 1969 : 38), the mid-Ordovician *L. decorticata* Cooper from the Elway Formation of Virginia, and *L. rideanensis* Cooper from the Aylmer Formation of Ontario (Cooper 1956 : 198, 203). All three species, however, are described as having an ornamentation consisting solely of fine concentric lines.

Lingulella collected from the Meadowtown and Rorrington Beds are indistinguishable in every respect (Tables 13, 14) and constitute *L. displosa* s.s. The small sample derived from the Stapeley Shales, on the other hand, differs significantly in the relative narrowness and very gentle biconvexity of the shell and in the trace of a fine median septum in the brachial valve. These differences have prompted the erection of a new taxon, but to indicate its essential affinity with the Meadowtown and Rorrington forms this is at the subspecific level only.

PALAEOGLOSSA Cockerell 1911 emended A. W.

1848 *Glossina* Phillips : 370 ; *non* Wiedemann 1830.
1911 *Palaeoglossa* Cockerell : 96.
1956 *Palaeoglossa* Cockerell ; Cooper : 194.
1965 *Palaeoglossa* Cockerell ; Rowell in Williams *et al.* : H270.

DIAGNOSIS. Elongately oval, biconvex lingulellinids ornamented by fine discontinuous fila with the dorsal pseudointerarea not differentiated into propareas.

DESCRIPTION. Elongately oval, biconvex lingulellinids with an acute curved ventral beak ; surface ornamented by fine fila in addition to growth lines ; ventral pseudointerarea slightly anacline divided by a narrow pedicle groove into striated propareas with strong flexure lines, dorsal pseudointerarea orthocline, striated, lenticular in outline and not divided into propareas ; low median ridge sporadically developed in the brachial valve ; muscle impressions unknown except for traces of a pair of umbonal muscle scars immediately anterior of the pseudointerareas of both valves.

TYPE SPECIES. *Lingula attenuata* J. de C. Sowerby in Murchison 1839.

TYPE HORIZON. Meadowtown Beds.

DISCUSSION. Well-preserved valves from the Meadowtown Beds afford an opportunity to learn more about the internal morphology of the topotypic *Lingula attenuata* Sowerby which is the type species of *Palaeoglossa* Cockerell (*nom. subst. pro Glossina* Phillips 1848). The presence and degree of differentiation of the pseudointerareas indicate that the genus is best accommodated among the Lingulellinae. Indeed in the absence of information about the principal muscle scars, *Palaeoglossa* differs from *Lingulella* only in details. They include the greater biconvexity, the more incurved beaks and the more elongately oval outline of *Palaeoglossa*, and possibly the skeletal structure, because the *Palaeoglossa* shell tends to be more laminar and its inner layers are not radially striated as in *Lingulella*. Differences between *Palaeoglossa* and *Pseudobolus* Cooper (1956 : 194) as currently understood are even more finely drawn ; and when the internal features of the latter genus become known, it may prove to be a junior synonym of *Palaeoglossa*.

Palaeoglossa attenuata (Sowerby) emended A. W.

(Pl. 3, figs. 2–13)

1839 *Lingula attenuata* Sowerby in Murchison : 641.
1866 *Lingula attenuata* Sowerby ; Davidson : 44.

DIAGNOSIS. Subequally biconvex *Palaeoglossa* with a brachial valve 73% as wide and 6% as deep as long and a pedicle valve 71% as wide and 7% as deep as long ; fila fine and discontinuous ; ventral pseudointerarea with a shallow narrow pedicle groove extending anteriorly for 11% of the length of the pedicle valve, and a dorsal pseudointerarea and low median ridge extending forward for 7% and 43% of the brachial valve length respectively.

DESCRIPTION. Subequally biconvex, elongately oval *Palaeoglossa* with curved lateral and rounded anterior margins, brachial valve 73% as wide as long and 6% as deep as long (with a range of 3% to 8% for 9 valves), pedicle valve 71% as wide as long and 7% as deep as long, both valves evenly convex in longitudinal and transverse profiles ; external surface ornamented by growth lines and fine discontinuous fila about 0·25 mm in wavelength ; ventral beak acutely incurved, dorsal beak obtusely rounded.

Ventral pseudointerarea striated, slightly anacline, crescentic in outline, 11% as long medially as the length of the valve, pedicle trough narrow and shallow ; divided umbonal muscle scars rarely impressed.

Dorsal pseudointerarea striated, almost orthocline, lenticular in outline and extending forward medially for 7% of the length of the valve (range 6% to 8% for 6 specimens) ; divided umbonal muscle scars rarely impressed on either side of a low variably developed median ridge extending anteriorly for 43% of the length of the valve (range 28% to 66% for 5 specimens).

FIGURED MATERIAL.

	length	width (mm)
External and internal moulds of brachial valve (BB 37109a, b)	11·0	8·0
External and internal moulds of pedicle valve (BB 37110a, b)	7·0	5·0
External and internal moulds of pedicle valve (BB 37111a, b)	12·5	8·7
Exterior of pedicle valve (BB 37112)	8·3	6·0
Exterior of pedicle valve (BB 37113)	6·5	4·5
External and internal moulds of brachial valve (BB 37114a, b)	13·0	9·0
Internal mould of pedicle valve (BB 37115)	16·0	–
External and internal moulds of pedicle valve (BB 37116a, b)	5·5	3·6
External and internal moulds of disarticulated valves (BB 37117a, b)	5·5	3·0
External and internal moulds of brachial valve (BB 37118a, b)	12·0	9·0

HORIZONS AND LOCALITIES. Meadowtown Beds : BB 37111, 37114 from outcrops on the Meadowtown–Rorrington road, 220 yds from Meadowtown Chapel (Grid Ref.

SJ 309012); BB 37113, 37115 from outcrops 80 yds from Meadowtown Quarry along Rorrington road (Grid Ref. SJ 311013); BB 37110 from outcrops along lane to Lower Ridge from benchmark 754, Little Weston (Grid Ref. SO 293984); BB 37109 from outcrops in Lower Wood Brook 400 ft south-east of the Meadowtown–Rorrington road (Grid Ref. SJ 307008); BB 37112 from laneside exposures 370 yds north of Meadowtown Chapel (Grid Ref. SJ 311015). Betton Beds: BB 37116, 37117 from outcrops downstream of junction between Holywell and Whitehouse Brooks (Grid Ref. SJ 303004); exact locality of BB 37116 uncertain. Rorrington Beds: BB 37118 from exposures in a stream 530 yds north-west of Meadowtown Chapel (Grid Ref. SJ 308017).

Palaeoglossa myttonensis sp. nov.

(Pl. 4, figs. 1–5)

DIAGNOSIS. Ventribiconvex *Palaeoglossa* with a brachial valve 78% as wide and 4% as deep as long and a pedicle valve about twice as deep; fila fine and normally continuous; dorsal pseudointerarea lenticular and restricted to the umbonal area, dorsal median septum extending anteriorly for about half the valve length; postero-medial internal surfaces of shell sporadically and shallowly pitted.

DESCRIPTION. Ventribiconvex, oval *Palaeoglossa* with curved lateral and rounded anterior margins; brachial valve 78% as wide and 4% as deep as long, pedicle valve about 8% as deep as long; both valves evenly convex in longitudinal and transverse profiles; surfaces ornamented by growth lines and fine, somewhat distant, more or less continuous fila with a wavelength of about 0·25 mm.

Ventral pseudointerarea striated, slightly anacline, crescentic, divided by a shallow pedicle trough extending anteriorly for 11% of the length of the valve.

Dorsal pseudointerarea striated, slightly anacline, lenticular in outline, restricted to the umbonal area and extending anteriorly for 9% of the valve length; dorsal median ridge low, extending forward for 51% of the valve length (range 47% to 54% for 5 specimens); postero-medial internal surfaces of both valves sporadically and shallowly pitted.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	External and internal moulds of conjoined valves (BB 37119)	–	4·5
PARATYPES	Incomplete external and internal moulds of brachial valve (BB 37121a, b)	–	–
	External and internal moulds of slightly disarticulated valves (BB 37122a, b)	6·5	5·0
	Internal mould of brachial valve (BB 37123)	6·5	5·2

HORIZON AND LOCALITIES. Mytton Flags: BB 37119, 37122 from tip heaps on road to Squilver 150 yds ENE of Whitegrit School (Grid Ref. SO 323976); BB 37121 from sides of adit of New Perkin's Level (Grid Ref. SJ 376022); BB 37123 from outcrops near the top of steep tributary to Crowsnest Dingle, 350 yds WNW from Blakemoorflat (Grid Ref. SJ 373008).

Discussion. Representatives of *Palaeoglossa* have been recovered from most formations constituting the Ordovician successions of the Shelve area, but samples giving some indication of the variability in the shape of the shell and the development of internal features have been obtained from only the Mytton Flags and the

Table 15

Statistics of length (l) and maximum width (w) of n brachial valves of *Palaeoglossa attenuata* (J. de C. Sowerby) from Meadowtown Beds (A) and the Rorrington Beds (B) and of *Palaeoglossa myttonensis* sp. nov. from the Mytton Flags (C)

	A	B	C
n	29	14	10
$\bar{l}$ mm (var l)	9·31 (11·789)	5·01 (16·285)	5·42 (2·813)
$\bar{w}$ mm (var w)	6·82 (6·243)	3·53 (7·37)	4·19 (1·93)
r	0·951	0·994	0·981
a (var a)	0·7277 (0·00186)	0·6727 (0·00045)	0·8283 (0·00321)

Table 16

Statistics of length (l) and maximum width (w) of n pedicle valves of *Palaeoglossa attenuata* (J. de C. Sowerby) from the Meadowtown Beds (A), the Rorrington Beds (B) and the Betton Beds (C)

	A	B	C
n	32	36	23
$\bar{l}$ mm (var l)	10·76 (28·081)	5·8 (11·584)	5·09 (1·589)
$\bar{w}$ mm (var w)	7·67 (17·835)	4·23 (6·518)	3·23 (0·67)
r	0·982	0·984	0·918
$\overline{\log_e l}$ (var $\log_e l$)	2·2667 (0·2173)	1·6098 (0·2958)	1·5978 (0·0594)
$\overline{\log_e w}$ (var $\log_e w$)	1·9051 (0·2646)	1·2872 (0·3104)	1·1431 (0·0618)
r_e	0·985	0·9871	0·925
α (var α)	1·1036 (0·0012)	1·0244 (0·00079)	1·0203 (0·00718)

Table 17

Statistics of length (l) and maximum depth (th) of 9 pedicle valves of *Palaeoglossa attenuata* (J. de C. Sowerby) from the Meadowtown Beds

$\bar{l}$ mm (var l)	10·34 (9·89)
$\overline{th}$ mm (var th)	0·77 (0·087)
r	0·964
a (var a)	0·094 (0·00008)

Table 18

Statistics of length (l) and length of ventral pseudointerarea (pl) of 7 pedicle valves of *Palaeoglossa attenuata* (J. de C. Sowerby) from the Meadowtown Beds

$\bar{l}$ mm (var l)	13·5 (66·00)
$\overline{pl}$ mm (var pl)	1·43 (0·789)
r	0·909
a (var a)	0·1093 (0·00041)

Betton, Meadowtown and Rorrington Beds. The Meadowtown assemblage is topotypic with those specimens on which J. de C. Sowerby (in Murchison 1839: pl. xxii, fig. 13) based *P. attenuata*. Comparisons of internal features like the relative anterior extension of the pseudointerareas and the dorsal median ridge, as well as the depth and outline of the valves (Tables 15–18), show that those *Palaeoglossa* recovered from the Betton and Rorrington Beds are indistinguishable from *P. attenuata*.

The small sample taken from the Mytton Flags, on the other hand, differs from the others in the significantly greater expansion in width relative to length during shell growth (Table 15). The beak of the brachial valve is also more acutely rounded and the lenticular pseudointerarea correspondingly more restricted to the umbonal region, while the sporadically distributed shallow pits indenting the postero-medial internal surfaces of the Mytton shells have not been seen in younger specimens. These differences merit specific recognition; and it is interesting to note that the new species appears to be restricted in stratigraphic distribution because the few specimens of *Palaeoglossa* known from the Weston, Spy Wood and Whittery Formations are best assigned to *attenuata*.

Subfamily **GLOSSELLINAE** Cooper 1956

PSEUDOLINGULA Mickwitz 1909 emended A. W.

1909 *Pseudolingula* Mickwitz: 771.
1945 *Pseudolingula* Mickwitz; Sinclair: 58.
1965 *Pseudolingula* Mickwitz; Rowell in Williams *et al.*: H267.
1969 *Pseudolingula* Mickwitz; Goryanski: 41.

DIAGNOSIS. Biconvex, parallel-sided glossellinids ornamented by fila with an orthocline ventral pseudointerarea divided by a pedicle groove into two striated propareas and an undifferentiated dorsal posterior margin; umbonal muscle scars divided, other muscle bases, including identifiable lateral and transmedian sets, supported on a broad adnate platform in the pedicle valve and impressed on either side of a median septum in the brachial valve; interiors sporadically pitted postero-medially.

DISCUSSION. Well-preserved internal moulds of *Pseudolingula* recovered from the Ordovician rocks of the Shelve area reveal more details of the internal morphology of this genus than have hitherto been recorded, and allow for a reappraisal of its position within the lingulide hierarchy. All characters confirm the lingulacean affinities of the taxon, and the divided aspect of the umbonal muscle bases indicates that it is best assigned to the Obolidae. This allocation is corroborated by the development of a pedicle groove bounded by flexures and striated propareas at least in the specimens from the Rorrington Beds. The undifferentiated dorsal posterior margin, however, suggests that *Pseudolingula* is closer to the Glossellinae than the Lingulellinae as currently conceived (see Rowell in Williams *et al.* 1965: H266–269), and its transference to the former subfamily is accordingly adopted for this study.

Pseudolingula spatula sp. nov.

(Pl. 4, figs. 6–14; Pl. 5, fig. 1; Text-fig. 4)

DIAGNOSIS. Subequally biconvex, subquadrate *Pseudolingula* with a brachial valve 67% as wide and 5% as deep as long, ornamented by strong fila laterally, becoming finer medially, and bearing an adnate ventral muscle platform and a strong dorsal median ridge arising up to one-fifth anteriorly of the beak and extending forwards 58% of the length of the valve.

DESCRIPTION. Subequally biconvex, subquadrate *Pseudolingula* with parallel lateral and obtusely rounded anterior margins and obtuse beaks with the more rounded dorsal one subtending an angle of about 100°; brachial valve 67% as wide and about 5% as deep as long; both valves subcarinate postero-medially but flattening laterally and anteriorly; external surface ornamented by growth lines and fila which are strongly developed with a wavelength of about 0·2 mm laterally but tending to become finer medially.

Ventral interior with median depression to accommodate pedicle but nature of the propareas unknown; umbonal muscles divided and represented by elongately oval scars on either side of the median depression, other muscle bases not identifiable individually but supported on a broad medially pointed platform, heavily rutted by growth lines and extending forward of the beak for about two-fifths of the length of the pedicle valves.

Dorsal interior with median depression at the beak but posterior margin undifferentiated; median septum arising up to one-fifth of the valve length anterior of the beak and becoming strong and relatively high at the anterior end which is, on average, 58% of the valve length forward of the dorsal beak (range 54% to 61% for

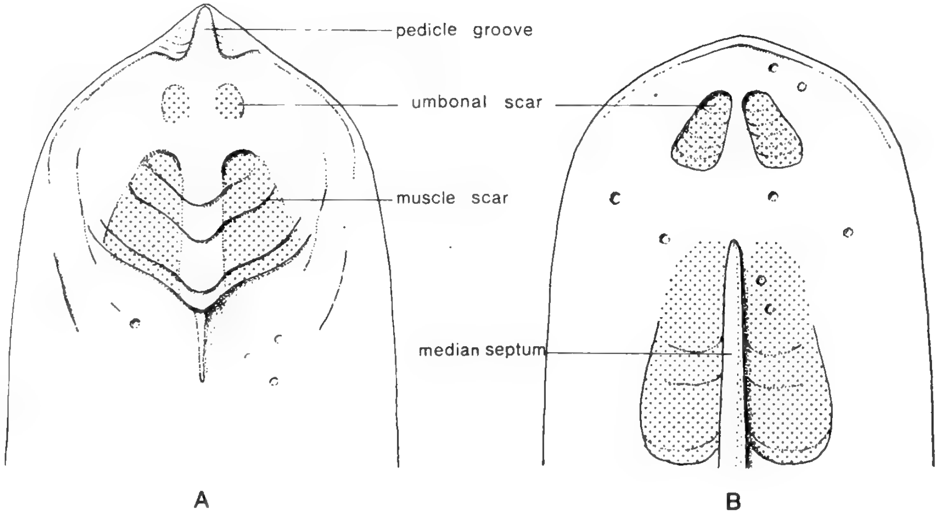


FIG. 4. Diagrammatic views of (A) the ventral and (B) the dorsal interiors of *Pseudolingula*.

3 specimens) ; muscle impressions including a pair of suboval umbonal scars situated submedially and a pair of long lateral and transmedian muscle scars inserted on either side of the median septum ; the two sets of scars extend anteriorly of the beak for 20% and 43% of the valve length respectively ; postero-medial internal surfaces of both valves sporadically and coarsely pitted.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	Incomplete external and internal moulds of brachial valve (BB 37124)	23·0	16·0
PARATYPES	External and internal moulds of brachial valve (BB 37125a, b)	10·5	6·5
	Internal mould of pedicle valve (BB 37126)	14·0	7·6
	External and internal moulds of brachial valve (BB 37128a, b)	13·5	9·0
FIGURED SPECIMEN	Incomplete exfoliated exterior of brachial valve (BB 37129)	–	7·6

TYPE HORIZON AND LOCALITIES. Weston Beds : BB 37124 from exposures in Cwm Dingle 640 yds south of Little Weston (Grid Ref. SO 294978) ; all other specimens from outcrops 210 yds south-east of road crossing Betton Dingle, Lyde (Grid Ref. SJ 317015).

DISCUSSION. *Pseudolingula* is known to occur sporadically throughout much of the Ordovician succession of the Shelve area, but only the Weston Beds have yielded a sufficient number of specimens to allow some estimates to be made of variability in the shape and internal structure of the shell. The valves known from other horizons must also be provisionally referred to the same species as the Weston material. Indeed an internal mould of a pedicle valve (BB 37130a, b) from the Rorrington Beds exposed in Deadman's Dingle, 90 yds from the junction with Spy Wood Dingle (Grid Ref. SO 289958), affords the only clear evidence of the nature of the ventral posterior margin (Pl. 4, fig. 11), while an incomplete ventral interior (BB 37129) from the Meadowtown Beds exposed at the side of Minicop Farm (Grid Ref. SJ 314018), and a badly exfoliated valve up to 15 mm long (BB 35583) from the Mytton Flags exposed in the River Camlad (Grid Ref. SO 320919), verify the stratigraphic persistence of the characteristic ventral muscle platform and concentric ornamentation (Pl. 4, figs. 12–14).

In the absence of quantitative data on shell outline and proportions in described *Pseudolingula*, the new species can only be distinguished, for the time being, by the

TABLE 19

Statistics of length (l) and maximum depth (w) of 18 brachial valves of *Pseudolingula spatula* sp. nov. from the Weston Beds

l mm (var l)	11·84 (39·16)
$\bar{w}$ mm (var w)	7·93 (16·775)
r	0·987
a (var a)	0·6545 (0·00067)

strong anterior development of the dorsal median septum and the strength and anterior configuration of the ventral muscle platform. In these aspects, the new species is certainly different from the type species, the mid-Caradocian *Pseudolingula quadrata* (Eichwald) from the U.S.S.R. (Goryanski 1969 : 41), as well as various Caradocian American forms (Sinclair 1945 : 59–62 ; Cooper 1956 : 215–217), and other differences may become apparent in due course.

Family **ELKANIIDAE** Walcott & Schuchert 1908

MONOBOLINA Salter 1865

Monobolina plumbea (Salter)

(Pl. 5, figs. 2–10 ; Pl. 6, fig. 1)

1859 *Lingula plumbea* Salter in Murchison : 50, foss. 8, fig. 1.
1865 *Monobolina plumbea* (Salter) Salter in Murchison : 334, pl. xiB, fig. 10.

DIAGNOSIS. Subelliptical *Monobolina* ornamented by fila and costellae numbering about 5 and 8 per mm respectively, 5 mm antero-medially of the umbo, and with well-developed muscle fields extending anteriorly for about half the valve length.

DESCRIPTION. Subelliptical, biconvex *Monobolina* with an evenly convex brachial valve averaging 78% as long as wide and 13% as deep as long and a slightly less convex pedicle valve tending to become flattened anteriorly in adult shells ; shell surface except for protegular areas ornamented by thin sharp fila and costellae in densities, 5 mm antero-medially of the umbones, of 3, 4, 5 and 6 fila per mm in 1, 2, 7 and 1 brachial valves, and of 7, 8 and 9 costellae per mm in 4, 7 and 2 brachial valves ; ventral pseudointerarea roughly lamellose, orthocline, averaging 72% of the width of the valve and 11% as long as the valve medially where it is divided by a strong pedicle groove 52% as wide as long, dorsal pseudointerarea poorly developed ; dorsal interior with a pair of variably impressed outside lateral and transmedial muscle scars situated submedially 44% of the valve length anterior of the dorsal umbo to form the postero-lateral boundaries to a pair of central muscle scars impressed medially at about the middle of the valve, *vascula lateralia* poorly defined ; ventral muscle platform low and solid with a convex boundary culminating in a subdued median ridge extending anteriorly for 46% of the valve length ; three pairs of scars representing the transmedian, middle lateral and anterior lateral muscles occurring on either side of the median ridge and flanked by a pair of anterior lateral impressions, *vascula lateralia* commonly well defined.

FIGURED MATERIAL.

	length	width (mm)
Internal mould of pedicle valve (BB 35467)	15·5	20·4
External mould of pedicle valve (BB 35468)	5·5	7·5
External and internal moulds of brachial valve (BB 35469a, b)	11·0	–
External and internal moulds of brachial valve (BB 35470a, b)	7·3	10·0
Internal mould of pedicle valve (BB 35471)	12·0	15·8
Internal mould of pedicle valve (BB 35472)	17·0	18·3
External and internal moulds of pedicle valve (BB 35473a, b)	12·5	–

HORIZON AND LOCALITIES. Mytton Flags: BB 35472 from adit entrance in Maddox's Coppice, 1200 yds ENE of St Luke's Church, Snailbeach (Grid Ref. SJ 382030); BB 35468 from sides of adit running into hillside at New Perkin's Level (Grid Ref. SJ 376022); BB 35469 from runnel just east of footpath to Blakemoorflat at head of Mytton Batch (Grid Ref. SJ 373006), BB 35470 from exposures in sunken cart track, west side of Snailbeach Coppice (Grid Ref. SJ 375026); BB 35471 from near top of steep tributary to Crowsnest Dingle 350 yds WNW of Blakemoorflat (Grid Ref. SJ 373008); BB 35467 from dump below Old Perkin's Level, Snailbeach (Grid Ref. SJ 376022); BB 35473 from dump outside adit in Perkin's Beach just below col separating Perkin's Beach and Mytton Batch (Grid Ref. SJ 366002).

DISCUSSION. The type species of *Monobolina* has been well known for over a century as an easily distinguishable inarticulate with a restricted stratigraphic and geographic range. Salter (1859: 56) based the species on specimens collected from Mytton Flags exposed west of the Stiperstones. Most of the specimens used in preparing this emended description are topotypic with his, and the remainder come from localities in the vicinity. They therefore afford an opportunity to present some reliable data on the morphologic variability of the species which illustrate the homogeneity as well as the distinctiveness of the taxon.

TABLE 20

Statistics of length (l) and maximum width (w) of 19 brachial valves of *Monobolina plumbea* (Salter)

$\bar{l}$ mm (var l)	8·82 (20·311)
$\bar{w}$ mm (var w)	11·29 (30·383)
r	0·979
a (var a)	1·2232 (0·00362)

TABLE 21

Statistics of length (l) and thickness (th) of 18 brachial valves of *Monobolina plumbea* (Salter)

$\bar{l}$ mm (var l)	10·37 (16·106)
$\overline{th}$ mm (var th)	1·39 (0·487)
r	0·927
$\overline{\log_e l}$ (var $\log_e l$)	2·2688 (0·1398)
$\overline{\log_e th}$ (var $\log_e th$)	0·216 (0·2251)
r_e	0·934
α (var α)	1·269 (0·0128)

TABLE 22

Statistics of length (l) and length of the lateral-transmedial muscle scars (sc) of 19 brachial valves of *Monobolina plumbea* (Salter)

$\bar{l}$ mm (var l)	11·57 (9·2)
$\overline{sc}$ mm (var sc)	5·16 (2·163)
r	0·903
a (var a)	0·4849 (0·00255)

TABLE 23

Statistics of valve length (l) and length of the entire muscle fields (ls) in 12 brachial valves of *Monobolina plumbea* (Salter)

$\bar{l}$ mm (var l)	12·89 (4·979)
$\overline{ls}$ mm (var ls)	6·69 (2·343)
r	0·943
$\overline{\log_e l}$ (var $\log_e l$)	2·5419 (0·0296)
$\overline{\log_e ls}$ (var $\log_e ls$)	1·8754 (0·0510)
r_e	0·943
α (var α)	1·3126 (0·0189)

TABLE 24

Statistics of length (l) and thickness (th) of 12 pedicle valves of *Monobolina plumbea* (Salter)

$\bar{l}$ mm (var l)	8·27 (17·045)
$\overline{th}$ mm (var th)	1·0 (0·306)
r	0·95
$\overline{\log_e l}$ (var $\log_e l$)	2·001 (0·2228)
$\overline{\log_e th}$ (var $\log_e th$)	−0·015 (0·0301)
r_e	0·972
α (var α)	0·3676 (0·00075)

TABLE 25

Statistics of valve length (l) and muscle platform length (sc) of 13 pedicle valves of *Monobolina plumbea* (Salter)

$\bar{l}$ mm (var l)	12·74 (12·778)
$\overline{sc}$ mm (var sc)	5·88 (3·235)
r	0·983
a (var a)	0·5032 (0.00079)

TABLE 26

Statistics of valve length (l) and pedicle groove length (pe) of 13 pedicle valves of *Monobolina plumbea* (Salter)

$\bar{l}$ mm (var l)	12·74 (12·778)
$\overline{pe}$ mm (var pe)	1·42 (0·288)
r	0·903
a (var a)	0·1502 (0·00035)

Family **PATERULIDAE** Cooper 1956

PATERULA Barrande 1879

Paterula cf. ***bohemica*** Barrande

(Pl. 6, figs. 2–11)

1879 *Paterula bohemica* Barrande : plate 152.

DIAGNOSIS. Elongately oval *Paterula* with a brachial valve 87% as wide as long and 17% as deep as long ; ventral beak submarginal, dorsal beak submarginal, 9% of the length of the brachial valve forward of the truncated posterior margin; limbus well developed.

Description. Dorsibiconvex, elongately oval *Paterula* with a slightly truncated posterior margin and a rounded anterior one, brachial valve with a mean width relative to length of 87% (range 82% to 90% for 7 valves) and a mean depth relative to length of 17% (range 15% to 20% for 5 valves), pedicle valve with a mean depth relative to length of 8% for 2 valves; surface ornamented by fine concentric lines; pedicle notch wide, immediately posterior of ventral beak; submarginal dorsal beak located, on average, 9% of the length of 3 brachial valves (range 7% to 10%) forward of their posterior margins and not constituting the greatest depth of the valve which is in mid-region.

Limbus well defined in both valves about 7% as wide as the valves are long; other internal features unknown except for two lines diverging from the ventral beak and bounding a faint median ridge.

Figured material.

	length	width (mm)
Exterior of pedicle valve (BB 35590)	1·6	1·5
Exterior of brachial valve (BB 35591)	1·8	1·6
Exterior of pedicle valve (BB 35592)	1·6	1·5
Exterior of pedicle valve (BB 35593)	1·6	1·4
Exterior of brachial valve (BB 35594)	1·9	1·9
Incomplete exterior of brachial valve (BB 35595)	–	1·9
External and internal moulds of pedicle valve (BB 35588a, b)	2·0	1·9
External and internal moulds of brachial valve (BB 35589a, b)	1·6	1·4

Horizons and localities. BB 35590 to 35595 inclusive from Meadowtown Beds exposed 100 yds south-east of Minicop farm (Grid Ref. SJ 315018); BB 35588, 35589 from Hope Shales exposed in Hope Dingle behind Hope Cottage (Grid Ref. SJ 338009).

Paterula cf. ***perfecta*** Cooper

(Pl. 6, figs. 12, 13)

1956 *Paterula perfecta* Cooper: 258.

Diagnosis. Elongately oval *Paterula* with a brachial valve 88% as wide as long and 20% as deep as long, ventral beak submarginal, dorsal beak 23% of the length of the brachial valve forward of the rounded posterior margin; limbus becoming subdued anteriorly.

Description. Dorsibiconvex, elongately oval *Paterula* with rounded posterior and anterior margins, brachial valve with a mean width relative to length of 88% (range 80% to 90%) and a mean depth relative to length of 20% (range 20% to 21%) for 4 valves; pedicle valve with a mean depth relative to length of 11% (range 10% to 11%) for 3 valves; surface ornamented by fine concentric lines; pedicle notch small, ventral beak submarginal, located on average 10% of the length of 3 pedicle valves (range 9% to 11%) forward of their posterior margins ; dorsal beak representing the highest point of the brachial valve located, on average, 23% of the length of 5 brachial valves (range 15% to 25%) forward of their posterior margins.

Limbus well defined in both valves except posteriorly where it becomes obscure, other internal features unknown except for the characteristic two lines diverging from the ventral beak.

FIGURED MATERIAL.

	length	width (mm)
Exfoliated exterior of pedicle valve (BB 35596)	2·0	1·8
Exfoliated exterior of brachial valve (BB 35597)	2·0	1·8

HORIZON AND LOCALITY. Spy Wood Grit exposed in Spy Wood Dingle (Grid Ref. SO 281959).

DISCUSSION. *Paterula* occurs sporadically throughout much of the Shelve succession, although only 3 samples were available for study and even they were too small for anything but the simplest statistical assessment of variability. They do show, however, that the Shropshire *Paterula* belong to two distinct species. In the older stock, as represented by the samples from the Hope Shales and Meadowtown Beds, the posterior margin tends to be flattened or truncated, the limbus is well developed and the dorsal beak is submarginal. Such features, with the exception of the first, are also characteristic of *P. bohemica*, figured by Barrande (1879 : plate 152) from the Llanvirnian Šárka Formation of Czechoslovakia. They are not developed in specimens recovered from the Spy Wood Grit which tend to have a limbus becoming obscure anteriorly and especially a dorsal beak located well forward of a rounded posterior margin. The Spy Wood sample is close to *P. perfecta* Cooper (1956 : 258) from the Pratt Ferry Formation of Alabama except in the strength of the limbus which is continuous in the American species.

Despite these differences, the Shelve *Paterula*, provisionally at least, are most appropriately compared with *P. bohemica* and *P. perfecta*, the former to embrace specimens from the Mytton Flags to the Rorrington Beds inclusive, the latter shells occurring in the Spy Wood Grit and Aldress Shales.

Order ACROTRETIDA Kuhn 1949

Suborder ACROTRETIDINA Kuhn 1949

Superfamily **ACROTRETACEA** Schuchert 1893

Family **ACROTRETIDAE** Schuchert 1893

APSOTRETA Palmer 1955

Apsotreta sp.

(Pl. 6, figs. 14, 15)

The complementary moulds of an acrotretid pedicle valve (BB 35565a, b), from the Mytton Flags exposed near Wood House (Grid Ref. SJ 338003), are the sole representatives of *Apsotreta* in the Shelve succession. The valve which had a subcircular commissure just under 3 mm in diameter was conical in profile and about two-fifths as deep as long with a planar apsacline pseudointerarea and an apical foramen; the mould of the pseudointerarea was not sufficiently well preserved medially to determine whether an intertrough existed. The ornamentation consisted exclusively of fine growth lines. Internally the parallel-sided apical process, so diagnostic of the genus, extended forward for about two-fifths of the length of the anterior slope between 2 pairs of simply disposed *vascula lateralia*; a pair of cardinal scars were impressed on the posterior surface.

The valve cannot be profitably compared with those of other described *Apsotreta*, but it is noteworthy that its occurrence greatly extends the stratigraphic range of the genus which had previously been regarded as restricted to the Upper Cambrian (Rowell in Williams *et al.*: H276).

CONOTRETA Walcott 1889

Conotreta stapeleyensis sp. nov.

(Pl. 6, figs. 16–21)

DIAGNOSIS. *Conotreta* with a gently convex brachial valve averaging 85% as long as wide and a conical pedicle valve 37% as deep as long with a procline pseudointerarea bearing a low deltoid arch; apical process transversely oval, submedial *vascula lateralia* not deeply divided.

DESCRIPTION. Medium-sized *Conotreta* with a very gently convex brachial valve averaging 85% as long as wide and 6% as deep as long (for 3 valves), and a conical pedicle valve averaging 37% as deep as long (for 3 valves); pseudointerarea well defined averaging 71% of the maximum width of 3 pedicle valves and procline or rarely nearly catacline in attitude, so that the beak with an apical foramen may be located forward of the posterior margin by as much as 20% of the valve length, pseudointerarea divided medially by low deltoid arch with a mean width of 30% of its length; dorsal beak small, situated at the posterior margin defined by an anacline pseudointerarea; external ornamentation consisting solely of fine growth lines.

Ventral interior with a pair of subcircular cardinal scars impressed posterolaterally of a transversely oval apical process, mantle canal system pinnate with the submedial branches of the *vascula lateralia* not deeply divided.

Dorsal interior with conspicuous propareas defined by a depressed median platform extending forward of the umbo for 18% of the length of the brachial valve and continuous with a long thin median septum of unknown profile; cardinal and anterior muscle scars forming a quadripartite pattern about the median septum and divergent *vascula lateralia* and extending anteriorly of the umbo for 56% of the valve length.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	Internal mould of pedicle valve (BB 35566)	2·5	3·0

		length	width (mm)
PARATYPES	External mould of brachial valve (BB 35567)	3·0	3·5
	Internal mould of brachial valve (BB 35568)	3·2	3·7
	Internal mould of brachial valve (BB 35569)	2·2	2·5
	Internal mould of brachial valve with adherent shell (BB 35570)	3·2	3·5
	External and incomplete internal mould of pedicle valve (BB 35571a, b)	3·5	3·7

HORIZON AND LOCALITY. Stapeley Shales exposed on the road side north-east of bench mark 412·5, Leigh Hall (Grid Ref. SJ 334036).

DISCUSSION. A small number of acrotetid moulds recovered from the Stapeley Shales appear to constitute a new species of *Conotreta*. In the absence of precise data, no comparison can be drawn between the Stapeley *Conotreta* and other described species in respect of the shape of the shell and its principal morphological features. However, a combination of some of the basic characters of the genus immediately separate *C. stapeleyensis* from American (Cooper 1956 : 247–255), Baltic (Goryanski 1969 : 62–65) and Scottish (Williams 1962 : 90) *Conotreta*. Such features include the development of a deltoid arch in place of an intertrough dividing a predominantly procline ventral pseudointerarea, and the late division of the submedial *vascula lateralia*.

The complementary moulds of a brachial valve which is likely to belong to *Conotreta* have also been found in the Hope Shales ; but, in the absence of an associated pedicle valve, its specific affinities cannot be determined.

Superfamily **DISCINACEA** Gray 1840

Family **TREMATIDAE** Schuchert 1893

SCHIZOCRANIA Hall & Whitfield 1875

Schizocrania salopiensis sp. nov.

(Pl. 6, figs. 22–26)

DIAGNOSIS. *Schizocrania* with subcircular brachial valve about one-third as deep as long with posteriorly placed umbo and dichotomizing radial capillae commonly 8 to 10 per mm, 5 mm antero-medially of umbo ; large posterior adductors extending anteriorly for one-third the length of the valve.

DESCRIPTION. Brachial valve subcircular and deep being 86% as long as wide and 33% as deep as long, transverse profile evenly convex, longitudinal profile asymmetrically convex with the posteriorly placed umbo overhanging a strong groove indenting the posterior part of the valve just within the smoothly rounded posterior margin ; exterior ornamented by sporadically occurring growth lines and capillae disposed radially from the umbo, curving to intersect the posterior margin, and branching by subequal dichotomy and commonly numbering 10 per mm, 5 mm antero-medially of the umbo ; dorsal interior with thickened rounded posterior margin extending postero-laterally for over four-fifths the width of the valve.

Dorsal interior with faint median ridge; posterior adductor scars large, suboval, slightly divergent and commonly with well-defined tracks, extending anteriorly of the posterior margin for 32% of the length of the valve; anterior adductor scars small, suboval, normally obscure, situated about half-way along the valve and more medially placed than posterior pair; a pair of short submedial fine ridges located forward of the anterior adductor scars may also represent muscle supports; pedicle valve unknown.

TYPE AND FIGURED MATERIAL.

		length	width (mm)
HOLOTYPE	External and internal moulds of brachial valve (BB 35358a, b)	11·0	13·5
PARATYPES	Exterior of brachial valve (BB 35359)	9·0	10·0
	External and internal moulds of brachial valve (BB 35360a, b)	1·9	2·3
	Exterior of brachial valve (BB 35361)	3·5	3·5
	External and internal moulds of deformed brachial valve (BB 35362a, b)	7·5	6·5
	External and internal moulds of brachial valve (BB 35404a, b)	4·2	5·0

HORIZONS AND LOCALITIES. BB 35358, 35359 from Spy Wood Grit exposures 1100 yds NNE of Rorrington (Grid Ref. SJ 303015); BB 35360 from Rorrington Beds exposed in Deadman's Dingle 100 ft upstream from its junction with Spy Wood Brook (Grid Ref. SO 280960); BB 35361, BB 35362 from Rorrington Beds exposed in tributary to Lower Wood Brook, 340 yds south-east of Desert (Grid Ref. SJ 308017); BB 35404a, b from Betton Beds exposed in a stream 330 yds WSW of Little Weston (Grid Ref. SO 290983).

DISCUSSION. Brachial valves of *Schizocrania* occur rarely in the pre-*gracilis* rocks of the Shelve area, but are fairly common in the Rorrington Beds and Spy Wood Grit which have provided the two small samples used to derive the statistics given in Tables 27–29. Comparisons of these estimates of dorsal outline and depth and of the anterior extension of the posterior adductor scars show a significant difference ($0{\cdot}05 > p > 0{\cdot}02$) only in the relatively greater depth of the Spy Wood valves. This difference may reflect the growth of a consistently shallower valve during Rorrington time. Two other smaller samples from the Betton and Meadowtown Beds also differ from the Spy Wood specimens only in the depth of the brachial valve which averaged 19% and 20% of the length of 4 and 5 brachial valves respectively. However, many *Schizocrania* from the Betton, Meadowtown and Rorrington Beds show signs of collapse induced by compaction of the shaly sediments in which they occur; and although there are no obvious signs of deformation in the specimens selected for measurement, the depressed condition of the valves which were mostly thin-shelled may yet prove to have been diagenetically induced.

Apart from the information provided in Tables 27–29, the two samples are also alike in the rounded outline of the posterior margin and in details of the dichotomizing radial ornamentation. Thus between 4 and 5 mm anterior of the umbo, 7, 8, 9, 10, 11 and 12 capillae per mm were counted respectively in 0, 1, 0, 3, 1 and 0 specimens from the Spy Wood Grit and in 1, 3, 3, 5, 1 and 1 specimens from the Rorrington Flags. The ribbing of the Betton and Meadowtown specimens shows a similar range in frequency and, although 3 valves from the Hope Shales, with counts of 10, 12 and 13 per mm, may be indicative of an older *Schizocrania* with finer radial ornamentation, the differences are not significant at present.

The Shropshire *Schizocrania* is closely related to *S. filosa* (Hall) which is known principally from the younger Trentonian rocks of N. America (Cooper 1956 : 275). No details are available on the variation in the general morphology of the American species. But the Shropshire forms are distinguishable in possessing a rounded rather than truncated posterior margin and a dorsal umbo which is not marginal: and although no pedicle valves have yet been recovered, these differences in the brachial valve seem sufficiently important to warrant the erection of a new species.

Table 27

Statistics of the length (l) and maximum width (w) of n brachial valves from the Spy Wood Grit (A) and the Rorrington Beds (B) of *Schizocrania salopiensis* sp. nov.

	A	B
n	6	20
$\bar{l}$ mm (var l)	6·42 (9·842)	4·29 (5·432)
$\bar{w}$ mm (var w)	7·23 (15·01)	5·1 (7·58)
r	0·997	0·986
a (var a)	1·2349 (0·00259)	1·1813 (0·0022)

Table 28

Statistics of the length (l) and depth (th) of n brachial valves from the Spy Wood Grit (A) and the Rorrington Beds (B) of *Schizocrania salopiensis* sp. nov.

	A	B
n	7	9
$\bar{l}$ mm (var l)	6·71 (8·822)	4·1 (3·74)
$\overline{th}$ mm (var th)	2·24 (1·233)	0·77 (0·145)
r	0·914	0·971
a (var a)	0·3739 (0·0046)	0·1969 (0·00032)

Table 29

Statistics of the length (l) and length of the posterior adductor scars measured from the umbo (sc) of n brachial valves from the Spy Wood Grit and the Rorrington Beds of *Schizocrania salopiensis* sp. nov.

	A	B
n	4	10
$\bar{l}$ mm (var l)	6·62 (14·23)	7·28 (12·984)
$\overline{sc}$ mm (var sc)	2·05 (1·397)	2·07 (1·193)
r	0·997	0·952
a (var a)	0·3133 (0·00033)	0·3031 (0·00107)

Family **DISCINIDAE** Gray 1840

Subfamily **ORBICULOIDEINAE** Schuchert & Le Vene 1929

ORBICULOIDEA d'Orbigny 1847

Orbiculoidea sp.

(Pl. 7, fig. 1)

An external mould with adherent shell of a brachial valve of *Orbiculoidea* (BB 35576) has been recovered from an unlocated exposure of Stapeley Shales. The valve which was 7 mm long and 1·2 mm deep was subcircular in outline with the beak situated about 2·5 mm forward of the slightly truncated posterior margin. The posterior sector was slightly concave, but the rest of the valve sloped evenly away from the beak to a flattened margin about 0·5 mm wide. The external surface was ornamented by fine fila ; no internal features are known.

No useful purpose is served in comparing this brachial valve with those of described species, many of which are similarly proportioned. The specimen however constitutes an interesting record as one of the earliest *Orbiculoidea* so far identified.

SCHIZOTRETA Kutorga 1848

Schizotreta transversa sp. nov.

(Pl. 7, figs. 2, 3, 7)

DIAGNOSIS. Subcircular *Schizotreta* slightly wider than long with a ventral beak located one-third of the valve length forward of the posterior margin and a surface ornament consisting solely of growth lines.

DESCRIPTION. Subcircular *Schizotreta* with a slightly truncated posterior margin, brachial valve very gently convex, pedicle valve subconical, almost nine-tenths as long as wide and just over one-fifth as deep as long, with an even slope away from the beak except for a slightly concave posterior margin and immediately in front of the slit-like pedicle opening ; dorsal beak submarginally located just over one-tenth forward of the posterior margin ; surface of both valves ornamented solely by fine growth lines ; interiors unknown.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	Exfoliated pedicle valve (BB 35577)	2·7	3·1
PARATYPES	Exfoliated pedicle valve (BB 35578)	4·5	5·0
	Exfoliated brachial valve (BB 35579)	4·5	–

TYPE HORIZON AND LOCALITIES. Meadowtown Beds : BB 35577, 35578 from exposures 80 yds from Meadowtown Quarry along the Rorrington road (Grid Ref. SJ 311012). BB 35579 from exposure in lane to Kinton, 200 yds west of Holy Trinity Church, Middleton (Grid Ref. SO 295993).

DISCUSSION. There seems to be little doubt that the discinid specimens collected from the Meadowtown Beds, and also a few less well-preserved moulds from the Rorrington Beds, should be assigned to *Schizotreta* because the beak of the brachial valve is located submarginally. In other features, however, especially the transversely oval outline and the absence of fila, the new species is unlike penecontemporaneous *Schizotreta* including the type species of the genus *S. elliptica* (Kutorga) from the Baltic area (Goryanski 1969 : 83), and Scottish and American stocks (Williams 1962 : 94–95 ; Cooper 1956 : 277–282). Only *S. microthyris* from the Oranda Formation of Virginia compares with *S. transversa* in outline although fila are finely but persistently developed on the American species and serve to distinguish the two.

Schizotreta sp.

(Pl. 7, fig. 4)

The external mould of a discinid pedicle valve (BB 35580), from the Mytton Flags exposed in the sides of the adit in the New Perkin's Level (Grid Ref. SJ 376022), has been provisionally identified as a *Schizotreta* rather than an *Orbiculoidea* mainly on the basis of its elongately oval outline and strong regular fila. The valve was 4·5 mm long and about two-thirds as wide and one-fifth as deep as long. The beak was located about one-third the length of the valve anteriorly of the curved posterior margin with the pedicle opening represented by a narrow slit, about 0·5 mm long, breaching the slightly concave posterior surface.

The valve is immediately distinguishable from *S. transversa* in its elongately oval outline and strong fila which, together with the relatively anterior location of the beak and pedicle opening, render the specimen different from most other described species. However, in view of the fact that no *Schizotreta* has previously been reported from Lower Ordovician rocks (Rowell in Williams *et al.* 1965 : H285), more information, especially about the brachial valve, is required before taxonomic recognition is warranted.

Suborder CRANIIDINA Waagen 1885

Superfamily **CRANIACEA** Menke 1828

Family **CRANIIDAE** Menke 1828

PETROCRANIA Raymond 1911

Petrocrania dubia sp. nov.

(Pl. 7, figs. 5, 6, 8)

Diagnosis. *Petrocrania* known only by its subquadrate, conical brachial valve with the greatest depth corresponding more or less to mid-point ; elevated anterior adductor scars larger than posterior.

Description. Exterior of brachial valve slightly irregular, subquadrate and suboval with flattened posterior margin, 82% as long as wide (mean for 4 valves) and 26% as deep as long (mean for 3 valves) with maximum depth at about mid-point ; surface with sporadic concentric growth lines, otherwise smooth ; shell with thickened slightly everted margin corresponding to limbus about 1 mm wide.

Interior of brachial valve with strongly impressed suboval postero-lateral adductor scars smaller than suboval elevated anterior adductor scars situated submedially up to 60% forward of the posterior margin and ornamented by fine parallel wavy ridges; mantle canal system pinnate with variably impressed sigmoidal *vascula lateralia.*

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	External and internal moulds of brachial valve (BB 35405a, b)	11·5	14·0

HORIZON AND LOCALITY. Whittery Shales: exposures in stream at north end of Spring Coppice 865 yds south-east of Hockleton Bridge (Grid Ref. SO 279997).

DISCUSSION. Although the sole craniid found in the Shelve area is represented by only 4 adult brachial valves from the Whittery Shales and a single immature brachial valve from the Aldress Shales, it is distinctive enough to be recognized as a new species. Its smooth slightly irregular external appearance suggests that it is best assigned to *Petrocrania* and the sigmoidal *vascula lateralia* impressed on the internal surface confirm this allocation. There are, however, two other internal features which are not typical of *Petrocrania.* They are the greater size of the anterior adductor scars compared with the posterior pair and the thickened margin. The new species, therefore, differs from other described *Petrocrania* in these characters. It is also distinctive in the mid-region location of the valve beak which is situated much nearer the posterior margin in American species of Ordovician age (Cooper 1956 : 287–291) and in *P. inexpectata* (Barrande 1848 : pl. 110, fig. V) from the Caradocian Zahořany Formation of Czechoslovakia.

Class *ARTICULATA* Huxley 1869

Order ORTHIDA Schuchert & Cooper 1932

Suborder ORTHIDINA Schuchert & Cooper 1932

Superfamily **ORTHACEA** Woodward 1852

Family **HESPERONOMIIDAE** Ulrich & Cooper 1936

HESPERONOMIA Ulrich & Cooper 1936

Hesperonomia sp.

(Pl. 7, figs. 9, 12)

The slightly deformed external and internal moulds (BB 35334a, b) of a brachial valve, collected from the Mytton Flags exposed between 50 and 55 yds down the lane from Woodside House (Grid Ref. SJ 337002), are representative of the genus *Hesperonomia* Ulrich & Cooper. The subquadrate gently concave valve was about 7 mm long and had an anacline interarea about one-seventh as long as the valve, and an open notothyrium. The ornamentation consisted of fine costellae, arising by intercalation with a density of 6 per mm, 5 mm antero-medially of the umbo, and segregated into narrow sectors by a thickening of every eighth to tenth rib. Internally a blade-like cardinal process was supported on a low notothyrial platform bounded by short divergent brachiophores and not prolonged anteriorly into a median ridge ; simple narrow sockets were obliquely developed between the hinge-line and the brachiophores.

The combination of orthacean cardinalia, an unequally parvicostellate radial ornamentation and gently concave profile leave no doubt that the valve must be assigned to *Hesperonomia* as currently interpreted. Yet the ornamentation is so different from the normal costellate condition of the genus as to bring into question the use of the convexity or concavity of the brachial valve to distinguish between *Hesperonomiella* and *Hesperonomia*. Thus although the Mytton specimen is like *Hesperonomia australis* Ulrich & Cooper (1938 : 116) from the Odenville Limestone of Alabama, it more closely resembles the Arenigian *Hesperonomiella carmalensis* Bates (1968 : 142) from Anglesey in every respect except that the brachial valve of the Welsh species is very gently convex. Indeed, the Shropshire specimen may have been more closely related to *H. carmalensis* than to American *Hesperonomia* because the profile of the brachial valve was not as stable as its use for generic identification implies.

Family **ORTHIDAE** Woodward 1852

Subfamily **ORTHINAE** Woodward 1852

ORTHIS Dalman 1827

Orthis cf. ***callactis*** Dalman 1828

(Pl. 7, figs. 10, 11, 13–16)

DIAGNOSIS. Transversely semi-oval, mucronate *Orthis* with a pedicle valve over one-third as deep as long and a planar brachial valve 57% as long as wide, ornamented by about 17 costae with a wavelength of about 0·8 mm, 5 mm antero-medially of the dorsal umbo.

DESCRIPTION. Plano-convex, transversely semi-oval *Orthis* with sharply acute cardinal angles and a pedicle valve, over one-third as deep as long, evenly convex in longitudinal profile but tending to become flattened postero-laterally ; mean length of 3 brachial valves 57% (range 52% to 60%) of the maximum width, slightly convex for the first 2 mm of growth with a shallow median sulcus but becoming plane and rectimarginate in later stages of growth ; ventral interarea short, about one-twelfth as long as the pedicle valve, strongly curved, apsacline ; dorsal interarea anacline, cardinal extremities acute at about 60° ; ornamentation consisting of about 17 angular costae, about 0·8 mm in wavelength 5 mm anterior of dorsal umbo, bearing fine lamellae and capillae ; postero-lateral sectors with about 5 short rugae disposed at an acute angle with the hinge-line.

Ventral interior with teeth supported by short dental plates extending anteriorly for about one-seventh the length of the pedicle valve, pedicle callist small, muscle field with a rounded anterior boundary about one-quarter as long as the pedicle valve, adductor scar wide and not enclosed by the submedial diductor lobes.

Dorsal interior with a simple cardinal process, short divergent brachiophores, and suboval adductor scars divided by a low median ridge and extending forward for about half the length of the brachial valve.

FIGURED MATERIAL.

	length	width (mm)
External moulds of conjoined valves (BB 35497)	5·2	8·0
Incomplete external and internal moulds of pedicle valve (BB 35498a, b)	5·0	–
Incomplete external and internal moulds of brachial valve (BB 35499)	2·0	–
External moulds of conjoined valves (BB 35500)	–	5·5

HORIZON AND LOCALITIES. Mytton Flags: BB 35498 from crag in the wood of Crowsnest Dingle, 500 yds north of Blakemoorflat (Grid Ref. SJ 374012); other specimens from exposures in the adit in Maddox's Coppice, 1200 yds ENE of St Luke's Church, Snailbeach (Grid Ref. SJ 382030).

DISCUSSION. The few moulds of *Orthis* s.s. recovered from the Mytton Flags are, when allowance is made for the small size of the shells which were rarely more than 5·5 mm long, best identified as *Orthis callactis* Dalman, the type species for the genus. Illustrations of Russian representatives of the species from strata of B_{III} age (Schuchert and Cooper 1932 : Pl. 2; Alichova 1953 : Pl. 1) show that adult shells were more subquadrate than semi-oval and the cardinal extremities less acute than those of the Mytton specimens. But growth lines indicate that during adult development there was an acceleration of forward growth relative to lateral increment and that the outline, profile and ornamentation of young shells rendered them indistinguishable from the Shropshire specimens.

Orthis sp.

(Pl. 8, fig. 1)

A few dorsal internal moulds from the Stapeley Volcanic Group, exposed 220 yds SSE of Whitsburn Cottage, Leigh (Grid Ref. SJ 332034), are best assigned to *Orthis*. The larger (BB 35425) which is 4 mm long and about 6·5 mm wide is the mould of a very slightly convex semicircular valve with squared cardinal angles which was ornamented by about 16 rounded costae and bore a linear cardinal process on a low notothyrial platform. The brachiophores, bounding the notothyrium and defining the narrow sockets, were short, widely divergent, and disposed at about the same angle as the almost hypercline interarea.

The rounded costae, the slight convexity and the squared cardinal extremities suggest that the specimens are not assignable to *O. callactis* Dalman. But it seems advisable to withhold systematic recognition until a sample of the pedicle valves has been recovered and more is known about the variability of the brachial valve.

LENORTHIS Andreeva 1955

Lenorthis cf. ***proava*** (Salter)

(Pl. 8, figs. 2–9)

1866 *Orthis calligramma* var. *proava* Salter : 336.
1868 *Orthis Carausii* [Salter ms.] Davidson : 315.
1869 *Orthis Carausii* [Salter ms.] Davidson : 229.
1869 *Orthis calligramma* var. *proava* Salter ; Davidson : 241.
1883 *Orthis Carausii* Salter ; Davidson : 182–184.
1968 *Lenorthis proava* (Salter) Bates : 146.

DIAGNOSIS. Semi-oval *Lenorthis* with a brachial valve 70% as long as wide and 17% as deep as long and a pedicle valve 31% as deep as long, ornamented by about 19 costae with a wavelength of 0·75 mm, 5 mm antero-medially of the dorsal umbo, and fine capillae ; ventral muscle scar suboval extending anteriorly for 32% the length of the pedicle valve.

DESCRIPTION. Ventribiconvex, transversely semi-oval *Lenorthis* with an evenly convex pedicle valve 31% as deep as long and a brachial valve 70% as long as wide and 17% as deep as long with a shallow sulcus extending antero-medially of the umbo for about 3 mm but becoming ill-defined thereafter ; ornamentation consisting of 15 to 20 narrowly rounded costae on 1, 1, 0, 1, 5 and 1 brachial valves more than 5 mm long, with a mean wavelength (and variance) of 0·75 mm (0·005), 5 mm anterior of the umbones of 9 brachial valves, bearing delicate capillae with those occurring medially in the interspaces tending to be stronger ; ventral interarea curved apsacline, about one-seventh as long as the pedicle valve ; dorsal interarea shorter anacline, cardinal extremities slightly acute or more rarely rectangular.

Ventral interior with strong teeth supported by narrowly divergent dental plates extending anteriorly for 17% of the length of the pedicle valve, pedicle callist small, ventral muscle field subcordate, 96% as wide as long, with the submedial diductor lobes slightly longer than the broad median adductor scar and extending anteriorly for 32% of the length of the pedicle valve ; ventral mantle canal system rarely impressed but with divergent *vascula media*.

Dorsal interior with ridge-like cardinal process, oblique sockets and short, rod-like brachiophores ; brachiophore bases extending anteriorly for about 14% of the length of the brachial valve and 49% as long as the lateral extension of the simple sockets ; dorsal adductor field quadripartite with the posterior pair of scars slightly larger, extending forward of the umbo for 56% of the length of the valve.

FIGURED MATERIAL.

	length	width (mm)
Internal and external moulds of pedicle valve (BB 35501a, b)	6·5	7·7
Internal and external moulds of pedicle valve (BB 35502a, b)	5·7	8·0
Internal and external moulds of brachial valve (BB 35503a, b)	5·3	8·0
Internal and external moulds of brachial valve (BB 35504a, b)	7·5	–

HORIZON AND LOCALITIES. Mytton Flags : BB 35501, 35502 from exposures in roots of felled tree 70 yds north of entrance to Yewtree Level, the Hollies, Snailbeach

(Grid Ref. SJ 380018); BB 35503, 35504 from crag in Perkin's Beach 170 yds west of Shepherd's Rock (Grid Ref. SO 372999).

Discussion. The most remarkable feature of the two biconvex, costate orthids recovered from the Ordovician rocks of Shelve is that, although they belong to two different genera from widely separate horizons, they are indistinguishable in most of the attributes that are used to discriminate between species (Tables 30–38). Such dimensional estimates are numerical expressions of the way certain exoskeleton proportions were maintained during growth. They indicate the remarkable stability of the primitive strophic shell commonly referred to as 'typically orthid'. But there is no doubt that the two stocks can immediately be separated by the disposition of the ventral *vascula media* which is the chief diagnostic difference between *Orthambonites* and *Lenorthis* (Williams in Williams *et al.* 1965 : H311–313).

Lenorthis proava was first described by Salter (1866 : 336) as a variety of *Orthis calligramma* Dalman from the Arenigian Carmel Grits of Anglesey. The type specimens have since been lost, but Bates (1968 : 147) has recently collected good samples from the same horizon. Comparisons between the Mytton and Anglesey shells show them to be the same in all morphological features except the costae which are significantly coarser in *L. proava* s.s. This difference alone is not considered sufficiently important to warrant taxonomic recognition. It is, moreover, noteworthy that other penecontemporaneous forms from Europe and eastern North America may also prove to be morphologically comparable with *L. proava*. The accounts given by Rubel (1961 : 173) of *'Orthambonites' orbicularis* (Pander) and of *'Orthis' panderiana* (Hall & Clarke) by Ulrich & Cooper (1938 : 102) suggest that these stocks are *Lenorthis* closely related to the British species and especially similar in the number of costae which appears to be the most reliable character for the differentiation of species. *L. parvicrassicostatus* (Cooper) from the Upper Ordovician of Scotland (Williams 1962 : 98) is also close to *L. proava* in the shape of its shell and the number of its costae, but the external surface is not capillate.

ORTHAMBONITES Pander 1830

Orthambonites exopunctata sp. nov.

(Pl. 8, figs. 10–17; see also Text-fig. 3, p. 24)

Diagnosis. Subcircular *Orthambonites* with the brachial valve 74% as long as wide and 18% as deep as long and a pedicle valve 31% deep as long, ornamented by about 15 costae pierced by radial rows of exopuncta, and with a wavelength of 0·8 mm, 5 mm antero-medially of the dorsal umbo; cordate ventral muscle scar extending anteriorly for 36% of the length of the pedicle valve, dorsal adductor scars impressed for 51% of the length of the brachial valve.

Description. Ventribiconvex, subcircular *Orthambonites* with the pedicle valve 31% as deep as long and evenly convex in transverse and longitudinal profiles; brachial valve 74% as long as wide and 18% as deep as long with a shallow median sulcus almost half as wide as the length of the valve but tending to die out anteriorly; ornamentation consisting of 14 to 16 subangular costae on 2, 4 and 3 brachial valves more than 5 mm long, with a mean wavelength (and variance) of 0·81 mm (0·005), 5 mm anterior of the umbones of 7 brachial valves, crossed by fine lamellae and perforated by a row of exopuncta on either side of each costal crest in both valves; ventral interarea curved, apsacline, about one-sixth as long as the pedicle valve; dorsal interarea anacline, shorter, cardinal extremities invariably obtuse in shells longer than 3 mm.

Ventral interior with blunt teeth rarely crenulated, supported by narrowly divergent dental plates extending anteriorly for 23% of the length of the pedicle valve, pedicle callist small, ventral muscle field cordate in adult valves 84% as wide as long with the submedial diductor lobes extending anteriorly for 36% of the length of the pedicle valve but not enclosing the shorter, medially divided, adductor scar; ventral mantle canal system saccate with proximal parts of *vascula media* adjacent.

Dorsal interior with ridge-like cardinal process, oblique sockets and short, rod-like brachiophores usually heavily encased in secondary shell, brachiophore bases extending anteriorly for 19% of the length of the brachial valve and 48% as long as the lateral extension of the simple sockets; dorsal adductor field quadripartite extending forward of the umbo for 51% of the length of the valve; dorsal mantle canal system not completely known but probably saccate.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	Exterior of brachial valve (BB 35371)	8·5	10·2
PARATYPES	Exterior of brachial valve (BB 35372)	7·4	9·0
	Internal mould of brachial valve (BB 35373)	7·8	9·6
	Internal and external moulds of brachial valve (BB 35374a, b)	4·5	–
	Internal mould of pedicle valve (BB 35375)	8·0	8·5
	Pedicle valve and internal mould (BB 35376a, b)	8·5	9·0

HORIZON AND LOCALITIES. Whittery Shales: BB 35374 from exposures in the lower part of the west bank of the River Camlad 60 yds north-east of Marrington Farm (Grid Ref. SO 272970); BB 35375 from exposures in Whittery Quarry at the south end of Whittery Wood, near Chirbury (Grid Ref. SO 275981); all other specimens from outcrops in a stream at the north end of Spring Coppice 865 yds south-east of Hockleton Bridge, near Chirbury (Grid Ref. SO 279997).

DISCUSSION. Like *Lenorthis proava* the Whittery *Orthambonites* is characterized by a shell that did not deviate significantly during growth from the modal orthid shape and proportions, even to the development of obtuse cardinal extremities in shells only 2·5 mm long (Tables 30–38). Moreover, although the new species differs from most congeneric stocks, including the penecontemporaneous American *O. bellus* (Cooper 1956 : 296) and *O. friendsvillensis* (Cooper 1956 : 303), in its significantly fewer ribs, in that character and all others that can be tested statistically it is indistinguishable from the Scottish Caradocian *O. playfairi* (Reed emended Williams 1962 : 97). The Whittery shells, however, are unique among all known *Orthambonites* in bearing a row of exopuncta on either side of each costa of both valves.

The exopuncta are shallow holes up to 0·2 mm deep, puncturing the external surface of the shell at acute angles directed posteriorly. Within 3 mm of the umbones of each valve, the exopuncta tend to occupy the crests of costae. In larger shells they alternate on either side of the crest line at intervals of about 0·5 mm, but become more closely crowded and approximate to a double row in the marginal zones of shells more than 7 mm long. Judging from the inferred arrangement of the mantle canals relative to the costal embayments they probably accommodated setae which dehisced at regular intervals as the shell grew forward to seal them off from the mantle edge in the manner described by Rudwick (1965 : 604) for *Acanthothiris*. If this interpretation is correct the arrangement and incidence of the exopuncta show that the growth of new setae not only balanced the loss of those isolated by shell deposition, but also compensated for the increasing expansion of the adult commissure as the decrease in forward growth tended to crowd the alternately arising setae into double rows which appeared more or less simultaneously. This pattern is different from that figured by Williams (in Williams *et al.* 1965 : H301) for *Orthambonites* cf. *rotundiformis* Cooper in which the morphology of the shell margin is compatible with the setal follicles having occupied narrow depressions in the intercostal eminences and not in the costal grooves. Such depressions are vestigial in *O. exopunctata*; but whether their presence is indicative of a more primitive anatomy as is suggested by their occurrence in Arenigian *Orthambonites* such as *O. calligramma* Dalman remains to be demonstrated.

TABLE 30

Statistics of length (l) and maximum width (w) of n brachial valves of *Orthambonites exopunctata* sp. nov. (A) and *Lenorthis* cf. *proava* (Salter) (B)

	A	B
n	17	20
$\bar{l}$ mm (var l)	4·97 (5·877)	4·8 (2·804)
$\bar{w}$ mm (var w)	6·74 (8·36)	6·84 (3·479)
r	0·984	0·867
$\overline{\log_e l}$ (var $\log_e l$)	1·497 (0·2132)	1·512 (0·1145)
$\overline{\log_e w}$ (var $\log_e w$)	1·8226 (0·1695)	1·886 (0·072)
r_e	0·985	0·873
α (var α)	0·892 (0·0016)	0·793 (0·00829)

TABLE 31

Statistics of length (l) and depth (th) of n brachial valves of *Orthambonites exopunctata* sp. nov. (A) and *Lenorthis* cf. *proava* (Salter) (B)

	A	B
n	13	8
$\bar{l}$ mm (var l)	6·55 (5·389)	5·84 (1·569)
$\overline{th}$ mm (var th)	1·18 (0·271)	0·99 (0·059)
r	0·863	0·617
a (var a)	0·224 (0·00117)	0·193 (0·0038)

Table 32

Statistics of length (l) and depth (th) of n pedicle valves of *Orthambonites exopunctata* sp. nov. (A) and *Lenorthis* cf. *proava* (Salter) (B)

	A	B
n	24	17
$\bar{l}$ mm (var l)	7·4 (5·892)	5·51 (3·441)
$\overline{th}$ mm (var th)	2·31 (0·674)	1·72 (0·2106)
r	0·919	0·578
a (var a)	0·338 (0·0008)	0·247 (0·00272)

Table 33

Statistics of length of pedicle valve (l) and length of ventral muscle scar (sc) for n specimens of *Orthambonites exopunctata* sp. nov. (A) and *Lenorthis* cf. *proava* (Salter) (B)

	A	B
n	22	16
$\bar{l}$ mm (var l)	7·79 (5·934)	5·71 (2·133)
$\overline{sc}$ mm (var sc)	2·77 (0·942)	1·81 (0·343)
r	0·939	0·906
a (var a)	0·399 (0·00094)	0·401 (0·00205)

Table 34

Statistics of length (l) and maximum width (w) of the ventral muscle scar of n specimens of *Orthambonites exopunctata* sp. nov. (A) and of *Lenorthis* cf. *proava* (Salter) (B)

	A	B
n	18	14
$\bar{l}$ mm (var l)	2·81 (0·789)	1·78 (0·299)
$\bar{w}$ mm (var w)	2·36 (0·426)	1·7 (0·174)
r	0·912	0·895
a (var a)	0·735 (0·00569)	0·763 (0·00966)

Table 35

Statistics of length of pedicle valve (l) and length of dental plates (dl) for n specimens of *Orthambonites exopunctata* sp. nov. (A) and of *Lenorthis* cf. *proava* (Salter) (B)

	A	B
n	21	16
$\bar{l}$ mm (var l)	7·23 (6·153)	5·75 (2·172)
$\overline{dl}$ mm (var dl)	1·68 (0·357)	0·98 (0·137)
r	0·923	0·895
$\overline{\log_e l}$ (var $\log_e l$)	1·996 (0·098)	1·717 (0·0636)
$\overline{\log_e dl}$ (var $\log_e dl$)	0·46 (0·1188)	−0·66 (0·1334)
r_e	0·926	0·903
α (var α)	1·101 (0·0091)	1·448 (0·0275)

TABLE 36

Statistics of length of brachial valve (l) and length of brachiophores at their bases (c) for n specimens of *Orthambonites exopunctata* sp. nov. (A) and of *Lenorthis* cf. *proava* (Salter) (B)

	A	B
n	8	13
$\bar{l}$ mm (var l)	6·16 (4·389)	5·6 (1·833)
$\bar{c}$ mm(var c)	1·19 (0·167)	0·8 (0·032)
r	0·971	0·729
a (var a)	0·195 (0·00036)	0·132 (0·00074)

TABLE 37

Statistics of length of brachiophores at their bases (l) and distances between the lateral edges of sockets (w) for n brachial valves of *Orthambonites exopunctata* sp. nov. (A) and *Lenorthis* cf. *proava* (Salter) (B)

	A	B
n	6	12
$\bar{l}$ mm (var l)	1·03 (0·111)	0·81 (0·034)
$\bar{w}$ mm (var w)	2·15 (0·347)	1·67 (0·09)
r	0·944	0·727
a (var a)	1·771 (0·0848)	1·637 (0·1262)

TABLE 38

Statistics of length of brachial valve (l) and length of adductor scar from umbo (sc) of n specimens of *Orthambonites exopunctata* sp. nov. (A) and of *Lenorthis* cf. *proava* (Salter) (B)

	A	B
n	8	7
$\bar{l}$ mm (var l)	6·16 (4·389)	5·46 (2·913)
$\overline{sc}$ mm (var sc)	3·13 (0·899)	3·06 (0·767)
r	0·967	0·948
a (var a)	0·453 (0·00221)	0·513 (0·0054)

Subfamily **PRODUCTORTHINAE** Schuchert & Cooper 1931

NICOLELLA Reed 1917

Nicolella cf. ***actoniae*** (J. de C. Sowerby)

(Pl. 9, figs. 1–6)

1839 *Orthis actoniae* J. de C. Sowerby in Murchison : 639.
1963 *Nicolella actoniae* (Sowerby) Williams : 352.

DIAGNOSIS. Plano-convex, mucronate *Nicolella* with a pedicle valve 32% as deep as long and a brachial valve 64% as long as wide, ornamented by 12 to 15 angular costae with a wavelength of about 1·1 mm, 5 mm antero-medially of the dorsal umbo ; costellae rare with 3ā arising first, cordate ventral muscle scar extending anteriorly for 34% of the length of the pedicle valve, dorsal adductor scars impressed for 48% of the length of the brachial valve.

DESCRIPTION. Plano- to slightly concavo-convex, subquadrate *Nicolella* with cardinal angles almost invariably acute in all growth stages, pedicle valve evenly convex 32% as deep as long and a brachial valve 64% as long as wide; ornamentation consisting of 12 to 15 angular costae in 2, 1, 2 and 2 brachial valves more than 8·5 mm long with a mean wavelength (with variance) of 1·09 mm (0·008) at 5 mm antero-medially of the umbones of 10 brachial valves, rarely branching in shells longer than 7·5 mm with 3ā usually arising first, concentric lamellae strong and continuous but not occurring regularly; ventral interarea short, curved orthocline; dorsal interarea very short, curved anacline.

Ventral interior with small blunt teeth supported by widely divergent dental plates extending anteriorly for 16% of the length of the pedicle valve, pedicle callist small, ventral muscle field cordate, slightly wider than long in adult valves with the submedial diductor lobes extending anteriorly for 34% of the length of the pedicle valve but not enclosing the shorter, undifferentiated median adductor scar.

Dorsal interior with ridge-like erect cardinal process, chilidial plates present, sockets slot-like defined by brachiophores extending laterally parallel to the hingeline for a distance equivalent to about one-third of the length of the brachial valve; dorsal adductor scars generally obscure but quadripartite with the larger anterior pair extending forward of the dorsal umbo for 48% of the length of 3 valves (range 46% to 50%).

FIGURED MATERIAL.

	length	width (mm)
External and internal moulds of brachial valve (BB 35327a, b)	3·0	5·5
External and internal moulds of brachial valve (BB 35328a, b)	10·0	15·0
External mould of brachial valve (BB 35329)	13·0	18·0
Incomplete internal mould of pedicle valve (BB 35330)	–	–
Internal mould of pedicle valve (BB 35331)	12·0	15·0

HORIZON AND LOCALITIES. Whittery Shales: BB 35327 from Whittery Quarry at south end of Whittery Wood near Chirbury (Grid Ref. SO 275981); BB 35328 from outcrops in west bank of the River Camlad 60 yds north-east of Marrington Farm (Grid Ref. SO 272970); BB 35329, 35331 from outcrops half way down the path going south from Marrington Farm to the valley bottom (Grid Ref. SO 272967); BB 35330 from outcrops in stream at north end of Spring Coppice 865 yds south-east of Hockleton Bridge (Grid Ref. SO 279997).

DISCUSSION. With the identification of the Whittery *Nicolella* as a form which is indistinguishable from the Actonian *N. actoniae* (J. de C. Sowerby), the remarkable morphological stability of that species becomes apparent, for it extends throughout the Upper Caradocian and Lower Ashgillian without significant change in any of its definable features (Williams 1963: 352–356, Wright 1964: 165–167). Tables 39–42 give the statistics for the main external and internal features of the Whittery specimens, and their comparison with similar data for *N. actoniae* from the Acton Scott Beds and the Portrane Limestone, and for *N. actoniae obesa* Williams from the Gelli-grin Calcareous Ashes, shows no significant difference in any of the listed characters. It is noteworthy that even in respect of the relative depth of the pedicle

Table 39

Statistics of length (l) and maximum width (w) of 9 brachial valves of *Nicolella* cf. *actoniae* (Sowerby)

$\bar{l}$ mm (var l)	7·93 (12·915)
$\bar{w}$ mm (var w)	12·37 (26·845)
r	0·978
a (var a)	1·4417 (0·0128)

Table 40

Statistics of length (l) and maximum depth (th) of 15 pedicle valves of *Nicolella* cf. *actoniae* (Sowerby)

$\bar{l}$ mm (var l)	11·53 (12·595)
$\overline{th}$ mm (var th)	3·66 (1·41)
r	0·854
a (var a)	0·3346 (0·00234)

Table 41

Statistics of length of pedicle valve (l) and length of ventral muscle scar (sc) for 12 specimens of *Nicolella* cf. *actoniae* (Sowerby)

$\bar{l}$ mm (var l)	12·79 (3·019)
$\overline{sc}$ mm (var sc)	4·29 (0·481)
r	0·802
a (var a)	0·3991 (0·00568)

Table 42

Statistics of length of pedicle valve (l) and anterior extension of dental plates (dl) of 7 specimens of *Nicolella* cf. *actoniae* (Sowerby)

$\bar{l}$ mm (var l)	11·73 (6·778)
$\overline{dl}$ mm (var dl)	1·91 (0·332)
r	0·964
a (var a)	0·2212 (0·0007)

valve the Whittery sample is intermediate between *N. actoniae* and the significantly deeper Bala subspecies and, when allowance is made for the variability of the samples, comparable with both in the inherent profile and rate of deepening of the pedicle valve.

The development of the ribbing does, however, indicate the much closer affinity with *N. actoniae* than with the Welsh subspecies. In the number and wavelength of costae the Whittery sample is like both *N. actoniae* and its subspecies. However, in all 8 brachial valves between 8·5 and 14·2 mm long, no costellae arise within 7·5 mm of the umbo and only 3 out of 8 valves show any branching, which consists solely of the appearance of $3\bar{a}$ in two specimens and $4\bar{a}$ arising before $3\bar{a}$ in the third. The Whittery sample is therefore more like *N. actoniae* in the rare development of costellae within the size range stipulated above, and also in being less thick-shelled than the Bala subspecies at such stages in growth (Williams 1963 : 356).

Only a few other remarks can be made about the Whittery shells. As in other *Nicolella*, muscle impressions are generally poorly defined. The ventral muscle field was wider than long in young shells, but during growth there was an acceleration in the anterior extension of the submedial diductor lobes so that the muscle field of adult pedicle valves tended to be longer than wide ; and the mean percentage width relative to length from the umbo (with variance) of 6 muscle impressions between 3·0 and 5·5 mm long was 109·4% (425·84).

Subfamily **WHITTARDIINAE** nov.

DIAGNOSIS. Plano- to concavo-convex orthids with a catacline to procline ventral interarea, disharmonic costellate ornamentation and open delthyrium and notothyrium ; ventral muscle field strongly bilobed with short parallel dental plates and three or four pairs of short ridges radiating from the muscle field boundary ; cardinalia consisting of a simple cardinal process and widely divergent brachiophores ankylosed to the hinge line, adductor scars subtriangular, divided into inner and outer pairs by *vascula myaria* ; ventral mantle canal system saccate, dorsal lemniscate to pinnate.

DISCUSSION. The new genus *Whittardia* represents an unexpected find within such well-known Ordovician successions as those of Shropshire, because although it is undoubtedly orthacean in its general organization and more particularly orthid in the bilobed nature of the ventral muscle field and the simplicity of the cardinalia, it is sufficiently unusual in a number of features to have aroused the attention of palaeontologists had it been discovered earlier. Among such features, the disharmonic ornamentation of the valves in the earlier stages of growth is the most bizarre. Judged on the umbonal region of adult moulds, dorsal valves, up to about 5 mm long, were convex and sulcate and ornamented by three symmetrically disposed pairs of strong costae radiating from the umbo. The only other ornamentation developed within 2 mm of the umbo, in all valves examined, consisted of fine closely-spaced lamellae. Thereafter at variable distances from the umbo intercalated costellae appeared, normally with a few thickened differentially. But with the relative loss in strength of the primary costellae in valves longer than 5 mm, the pattern became more evenly multicostellate with the costae arising by dichotomy or intercalation and interrupted by fine concentric lamellae which were especially conspicuous in the postero-lateral sectors free of ribs. The umbonal surface of the pedicle valve, on the other hand, appears at first sight to have been quite different, although details are usually obscured by the presence of a large mesothyridid foramen and the irregularity of the surface. The first-formed part of the preserved external mould, for about 2 mm anterior of the foraminal edge, appears to be flat and smooth and although valves up to about 5 mm long were sufficiently carinate to accommodate the dorsal sulcus they were evenly and closely costellate and without sign of accentuated interspaces corresponding to the strong costae of the brachial valve. In the ventral interior, however, there were three or four pairs of low narrow ridges radiating from the boundaries of the ventral muscle field and dying out peripherally, which could well have been complementary to the accentuated costae of the brachial valve. This arrangement suggests that the valves were imperfectly matched along the commissure, and such a loose fit is compatible with the weak articulation indicated by the simplicity of the teeth, the shallowness of the sockets, and the powerful development of the adductor musculature as inferred from the wide ventral impression and the deep posterior insertion of the dorsal attachment areas.

The other unusual features of the new genus are the catacline to procline ventral interarea and the profile of the brachial valve. The disposition of the ventral interarea was not unique among orthaceans but it was associated with a large mesothyridid foramen which must have accommodated a thick pedicle that was so short as to bring the pedicle valve into contact with the substratum ; the irregular contours of the valve are not *post mortem* features but expressions of growth in a physically restrictive environment. The longitudinal profile of the brachial valve was initially convex, but beyond the 2 mm growth stage the valve became gently concave. This attitude, however, was accentuated or reversed along a few narrow arcs resembling concentric rugae or, if incomplete, incipient geniculation. Such bands corresponded to only vague concentric indentations in the ventral interior, again indicative of the degree to which the valves grew independently of each other at the edges.

No other described orthacean compares closely with *Whittardia* : indeed the principal difficulty is deciding the suprageneric group to which it is best assigned. There is a superficial resemblance to the dinorthid *Plesiomys* (*Retrosistria*) in the ventral muscle impression but this is due to the catacline attitude of the ventral interarea in both stocks. Yet the simplicity of the cardinalia, and the bilobed nature of the ventral muscle scar and the mantle canal systems, suggest that the ancestor of *Whittardia* was more likely to have been an orthid and, provisionally at least, a monotypic subfamily of the Orthidae has been created to accommodate the new genus.

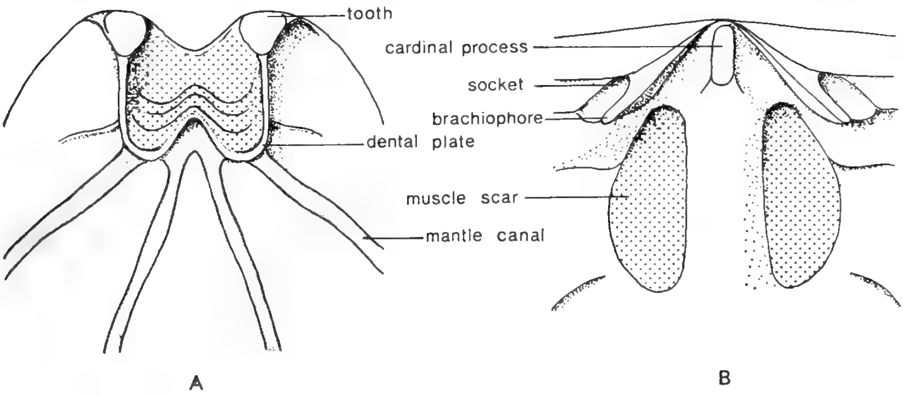


FIG. 5. Diagrammatic views of (A) the ventral and (B) the dorsal interiors of *Whittardia*.

Genus *WHITTARDIA* nov.

NAME. In honour of the late Professor W. F. Whittard.

DIAGNOSIS. Subquadrate to semi-elliptical, sulcate shell with an irregularly convex, carinate pedicle valve and a brachial valve initially convex but becoming concave in adult stages of growth ; radial ornamentation of both valves costellate, interrupted by fine lamellae, but with the finely lamellose umbonal region of the brachial valve bearing only 6 symmetrically disposed accentuated costae becoming subdued anteriorly ; ventral interarea gently curved catacline to procline, with wide open delthyrium and mesothyridid foramen, dorsal interarea very short, anacline, notothyrium open ; shell probably impunctate.

Ventral interior with widely divergent tooth ridges and flat, oblique teeth supported by short receding subparallel, widely spaced dental plates, postero-laterally enclosing a bilobed muscle field with a relatively short undifferentiated adductor scar separating divergent submedial diductor lobes which encroach onto a pair of divergent *vascula media* ; ventral mantle canal system probably saccate with *vascula media* branching early ; 3 or 4 pairs of narrow, low ridges radiate from the boundary of the muscle field and die away peripherally.

Dorsal interior with simple cardinal process elevated above a shallow notothyrial platform and wide short median ridge ; brachiophores short, widely divergent, ridge-like, scarcely elevated above hinge-line and postero-laterally defining a pair of elliptical sockets ; adductor scars subtriangular with posterior apices deeply inserted in the notothyrial platform and divided into outer and inner sets by obliquely disposed *vascula myaria* ; dorsal mantle canal pattern lemniscate or pinnate.

TYPE SPECIES. *Whittardia paradoxica* sp. nov. from the Whittery Shales, Shropshire.

Whittardia paradoxica sp. nov.

(Pl. 9, figs. 7–15 ; Pl. 10, figs. 1, 2, 4 ; Text-fig. 5)

DIAGNOSIS. Concavo-convex, subquadrate sulcate *Whittardia* with a pedicle valve 34% as deep as long and a brachial valve 79% as long as wide, ornamented by multicostellae with counts of 3 or 4 ribs per mm, 5 mm antero-medially of the dorsal umbo ; ventral and dorsal muscle scars extending anteriorly for 24% and 46% of their respective valve lengths.

DESCRIPTION. Variably subquadrate, sulcate *Whittardia* with a convex medially carinate pedicle valve with a mean length relative to width of 66% (range 56% to 83%) and a mean depth relative to length of 34% (range 26% to 41%) for 4 valves, and an irregularly concave brachial valve averaging 79% as long as wide (range 71% to 84%) for 4 valves ; radial ornamentation becoming multicostellate by intercalation and dichotomy in adult shells with 3 and 4 ribs per mm, 5 mm antero-medially of the umbones of 2 brachial valves in each case.

Ventral interior with bilobed ventral muscle scar becoming longer than wide in adult shells and extending forwards for an average of 24% of the length of 4 pedicle valves (range 20% to 33%).

Dorsal interior with cardinalia consisting of a simple cardinal process and widely divergent brachiophores extending forwards for an average of 17% (range 14% to 19%) of the length of 4 pedicle valves and supported by a shallow notothyrial platform; dorsal adductor scars subtriangular, deeply impressed posteriorly on either side of a short low median ridge, and extending forwards for 46% (range 42% to 51%) of the length of 4 brachial valves.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	Internal and external moulds of brachial valve (BB 35381a, b)	6·5	7·5
PARATYPES	Internal and external moulds of pedicle valve (BB 35382a, b)	11·5	14·0
	Internal and external moulds of pedicle valve (BB 35383a, b)	7·5	–
	Internal and external moulds of brachial valve (BB 35384a, b)	8·0	–
	Internal mould of brachial valve (BB 35385)	7·2	–
	Internal mould of pedicle valve (BB 35386)	7·5	–
	External and internal moulds of brachial valve (BB 35402a, b)	7·0	–
	External and internal moulds of pedicle valve (BB 35403a, b)	7·0	–

HORIZON AND LOCALITIES. Whittery Shales: BB 35384 from outcrops in stream at north end of Spring Coppice, 865 yds south-east of Hockleton Bridge (Grid Ref. SO 279997); all other specimens from Whittery Quarry at the south end of Whittery Wood, near Chirbury (Grid Ref. SO 275981).

DISCUSSION. The sample of *Whittardia paradoxica* available for assessing the morphological variation within the species was too small to estimate proportional growth, but statistics incorporated in the description were calculated for valves between 3 and 12·4 mm in length and give some idea of the variability.

Family **DOLERORTHIDAE** Öpik 1934

Subfamily **DOLERORTHINAE** Öpik 1934

DOLERORTHIS Schuchert & Cooper 1931

Dolerorthis cf. ***tenuicostata*** Williams

(Pl. 10, figs. 3, 5, 7, 10, 13)

1955 *Dolerorthis tenuicostata* Williams in Whittington & Williams: 406.

The incomplete external and internal moulds of a brachial and pedicle valve (BB 35459a, b; BB 35460a, b) of *Dolerorthis* have been collected from the Whittery Shales exposed in Whittery Quarry in the south end of Whittery Wood, near Chirbury (Grid Ref. SO 275981). The shell was ventri-biconvex with a pedicle valve about one-fifth as deep as long, sloping evenly away from the beak, and a very gently convex, transversely semi-oval brachial valve just over two-thirds as long as broad and lacking a sulcus. The ventral interarea was strongly apsacline and, at one-eighth the length of the pedicle valve, longer than the anacline dorsal interarea ; both delthyrium and notothyrium were open. The ornamentation consisted of microscopic concentric lamellae superimposed on fine costellae numbering 4 and 5 per mm at 5 mm antero-medially of the umbones, with costellae, mainly branching internally, arising early so that about 60 occur at the 5 mm growth stage and 75 at the margin of the brachial valve 8·5 mm long.

A pair of dental plates extending forward for about one-seventh the length of the pedicle valve defined the umbonal cavity which was occupied by a subtriangular muscle field with a relatively broad median adductor track ; only proximal traces of the *vascula media*, separated by a short median ridge, are preserved.

The cardinalia consisted of a narrow ridge-like cardinal process and sharp, divergent, unsupported brachiophores extending forward for one-fifth of the length of the brachial valve ; only faint impressions of a pair of suboval adductor scars are preserved on either side of a low median ridge becoming indistinct anteriorly.

The fineness of the ribbing as well as the internal features indicate that the Whittery *Dolerorthis* resembles *D. tenuicostata* (Williams 1955 : 406) from the Derfel Limestone of N. Wales. There are, however, some differences especially in the lesser convexity of the brachial valve of the Whittery species which also lacks a sulcus. These differences may ultimately prove to be taxonomically important.

Subfamily **GLYPTORTHINAE** Schuchert & Cooper 1931

GLYPTORTHIS Foerste 1914

Glyptorthis viriosa sp. nov.

(Pl. 10, figs. 6, 8, 9, 11, 12, 14, 15 ; Pl. 11, figs. 1, 2, 4)

DIAGNOSIS. Small *Glyptorthis* with a shallowly sulcate brachial valve about four-fifths as long as wide and a catacline pedicle valve 37% as deep as long, ornamented by fascicostellae numbering 2 or 3 per mm, 5 mm antero-medially of the dorsal umbo, and concentric lamellae with a modal density of 3 per mm between 5 and 6 mm antero-medially of the dorsal umbo.

DESCRIPTION. Subcircular, ventribiconvex *Glyptorthis* with roundly obtuse cardinal angles ; pedicle valve sharply carinate and 37% as deep as long, brachial valve 80% as long as wide and 23% as deep as long with a persistent rounded median sulcus, up to half as wide as the valve length, flanked by evenly convex lateral areas ; ventral interarea catacline to slightly apsacline, about one-third as long as the valve, with narrow delthyrium with subparallel boundaries ; dorsal interarea anacline with an open notothyrium ; radial ornamentation fascicostellate with ribs branching almost exclusively internally in the first four sectors and numbering 2 and 3 per mm, 5 mm antero-medially of the umbones of 3 brachial valves in each case ; concentric ornamentation consisting of strongly developed lamellae with counts of 3 and 4 in 3 and 1 valves between 5 and 6 mm antero-medially of the umbones.

Small trigonal teeth supported by narrowly divergent dental plates extending forward for 20% of the length of the pedicle valve; ventral muscle scar normally elongately pentagonal, with relatively wide median adductor scars flanked by somewhat shorter diductor scars, wider than long in young valves but becoming much more elongate in adult shells with a mean width of 97% of the length and extending anteriorly for 38% of the length of the valve.

Cardinal process simple and blade-like, brachiophores divergent and pointed with the secondary shell, forming the boundaries of the denticulate sockets and notothyrium, elevated above the brachial valve floor to simulate fulcral plates; convergent brachiophore bases extending forward for 19% of the valve length and 48% as long as wide; adductor muscle field quadripartite with a pair of suboval scars impressed on either side of the median ridge and extending anteriorly of the umbo for 52% of the length of the valve.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	External and internal moulds of brachial valve (BB 35505a, b)	4·7	6·0
PARATYPES	External and internal moulds of pedicle valve (BB 35506a, b)	4·5	5·5
	Internal mould of pedicle valve (BB 35507)	5·0	6·5
	Internal and incomplete external moulds of brachial valve (BB 35508a, b)	5·5	7·5
	Internal mould of pedicle valve (BB 35509)	6·5	7·0

TYPE HORIZON AND LOCALITY. All specimens from exposures of Spy Wood Grit, 1100 yds NNE of Rorrington (Grid Ref. SJ 303015).

DISCUSSION. Remains of *Glyptorthis* have been recovered from the Meadowtown Beds, Whittery Shales and Spy Wood Grit, but are common only in the last-named formation which has furnished the sample used in establishing a new species most closely related to *G. nantensis* McGregor (1961 : 187) from the Upper Llandeilo of the Berwyn Hills. However, even in the absence of precise information about the variability of the Welsh species, its pedicle valve is obviously not only much deeper but is further characterized by an interarea which is 'slightly apsacline, almost orthocline', and a significantly larger muscle scar.

Other penecontemporaneous Ordovician species from Ireland, Scotland and N. America also differ greatly. According to data kindly provided by Mrs H. Carlisle, in the brachial valve of *G. crispa* M'Coy from the Tramore Limestone of Ireland the cardinalia were relatively wider while the ventral muscle scar extended anteriorly more slowly during growth than in the Shropshire species. *G. balclatchiensis* (Davidson) from the Ardmillan Series of Scotland (Williams 1962 : 109), and *G. assimilis* Cooper (1956 : 361) from the Lower Ridley of Tennessee, both differ in being significantly wider. The former species also differs in the replacement of the dorsal sulcus by a narrow rounded fold during adult stages of growth, and the latter in being more coarsely imbricate.

Specimens of *Glyptorthis* recovered from the Whittery Shales and Meadowtown Beds may, provisionally at least, be referred to the new species despite minor differences in morphology.

The few moulds known from the younger formation include only one external mould of a brachial valve large enough to provide data about ornamentation. Counts of 2 per mm at 5 mm antero-medially of the umbo were obtained for both radial and concentric ornamentation and are smaller than those for *G. viriosa* s.s. In all other features, however, the shells must have been indistinguishable from the Spy Wood forms and more information is necessary to establish the significance of the difference.

The more frequently occurring *Glyptorthis* from the Meadowtown Beds, on the other hand, is identical with the new species except for the size of the cardinalia which extend anteriorly for only 10% of the length of the two known brachial valves. This size relationship is subnormal for brachial valves of comparable length in the Spy Wood sample, although more specimens are needed to assess the significance of the difference. Two specimens are figured (Pl. 10, fig. 15; Pl. 11, figs. 1, 2, 4): a brachial valve (BB 35520a, b) from loose flags by the side of Minicop Farm (Grid Ref. SJ 314018), and a pedicle valve (BB 35521a, b) from Quinton's Quarry in the field 200 yds north-east of Meadowtown Chapel (Grid Ref. SJ 312013).

TABLE 43

Statistics of length (l) and maximum width (w) of 17 brachial valves of *Glyptorthis viriosa* sp. nov.

$\bar{l}$ mm (var l)	4·23 (3·037)
$\bar{w}$ mm (var w)	5·26 (3·424)
r	0·978
$\overline{\log_e l}$ (var $\log_e l$)	1·3637 (0·1567)
$\overline{\log_e w}$ (var $\log_e w$)	1·6029 (0·1165)
r_e	0·981
α (var α)	0·8621 (0·00191)

TABLE 44

Statistics of length (l) and maximum depth (th) of 19 brachial valves of *Glyptorthis viriosa* sp. nov.

$\bar{l}$ mm (var l)	4·28 (3·05)
$\overline{th}$ mm (var th)	0·97 (0·162)
r	0·866
a (var a)	0·2306 (0·00078)

TABLE 45

Statistics of length (l) and maximum depth (th) of 23 pedicle valves of *Glyptorthis viriosa* sp. nov.

$\bar{l}$ mm (var l)	3·46 (4·857)
$\overline{th}$ mm (var th)	1·27 (0·594)
r	0·945
a (var a)	0·3497 (0·00061)

Table 46

Statistics of length (l) and length of dental plates (dl) in 20 pedicle valves of *Glyptorthis viriosa* sp. nov.

$\bar{l}$ mm (var l)	3·94 (4·674)
$\overline{dl}$ mm (var dl)	0·81 (0·246)
r	0·952
a (var a)	0·2293 (0·00027)

Table 47

Statistics of length (l) and length of ventral muscle scar (sc) in 22 pedicle valves of *Glyptorthis viriosa* sp. nov.

$\bar{l}$ mm (var l)	3·94 (4·848)
$\overline{sc}$ mm (var sc)	1·49 (1·124)
r	0·989
$\overline{\log_e l}$ (var $\log_e l$)	1·237 (0·2711)
$\overline{\log_e sc}$ (var $\log_e sc$)	0·1948 (0·4092)
r_e	0·994
α (var α)	1·2285 (0·00095)

Table 48

Statistics of length (l) and width (w) of the ventral muscle scar in 23 pedicle valves of *Glyptorthis viriosa* sp. nov.

$\bar{l}$ mm (var l)	1·46 (1·088)
$\bar{w}$ mm (var w)	1·42 (0·282)
r	0·932
$\overline{\log_e l}$ (var $\log_e l$)	0·1772 (0·4098)
$\overline{\log_e w}$ (var $\log_e w$)	0·2866 (0·1305)
r_e	0·957
α (var α)	0·5642 (0·00126)

Table 49

Statistics of length (l) and length of brachiophore bases (lc) in 19 brachial valves of *Glyptorthis viriosa* sp. nov.

$\bar{l}$ mm (var l)	4·62 (2·227)
$\overline{lc}$ mm (var lc)	0·86 (0·084)
r	0·865
a (var a)	0·1938 (0·00055)

Table 50

Statistics of length (l) and maximum lateral extension (w) of the brachiophore bases in 18 brachial valves of *Glyptorthis viriosa* sp. nov.

$\bar{l}$ mm (var l)	0·86 (0·088)
$\bar{w}$ mm (var w)	1·78 (0·274)
r	0·842
a (var a)	1·762 (0·05665)

Family **ALIMBELLIDAE** Andreeva 1960 emended A. W.

Diagnosis. Biconvex, smooth to capillate, uniplicate orthaceans with well-developed curved interareas and open delthyrium and notothyrium ; ventral muscle field impressed on pseudospondylium, dental plates absent at least in adult shells ; blade-like cardinal process and strong brachiophores supported by variably developed notothyrial platform ; ventral mantle canal pattern saccate, dorsal digitate.

Discussion. This family was erected by Andreeva (1960 : 292) to include two Tremadocian genera from the Urals, *Alimbella* Andreeva 1960 and *Medesia* Andreeva 1960 which were considered by her to be aberrant porambonitaceans, a conclusion accepted by Biernat (in Williams *et al.* 1965 : H530), in her review of the Syntrophiidina for the *Treatise on Invertebrate Paleontology*. In her discussion of the affinities of the Russian genera, Andreeva conceded that the morphology of the brachial valves is typically 'orthoid, similar to *Platystrophia*' (1960 : 292) but believed the organization of the pedicle valve to be so decisively porambonitacean as to preclude any connection with the orthaceans. It is difficult to understand how Andreeva came to this conclusion unless she had attached an overriding importance to the uniplicate condition of the shell which is certainly much more characteristic of the porambonitaceans than the orthaceans. Yet, if the ventral sulcus is ignored, the pedicle valves of both genera are immediately seen to be unexceptionally orthacean in the strong development of the interareas, the arrangement of the ventral muscle fields, and above all in the saccate mantle canal systems, with the proximal parts of the *vascula media* disposed medially in a manner which is unknown among the digitate porambonitaceans. The pseudospondylium is admittedly a rare feature among orthaceans but is known to have developed independently in several articulate groups and is, in any event, as well defined in the orthid *Glossorthis* as it is among the alimbellids.

All other features displayed by the Russian genera, such as the cardinal process and lack of brachiophore supports, are much more, but not exclusively, characteristic of the orthaceans rather than the porambonitaceans. It therefore seems reasonable to transfer the family to the Orthacea and to regard the stocks assigned to it as bearing the same relationship to the Orthidae as the Platystrophiinae do to the Plectorthidae and Finkelnburgiidae.

ASTRABORTHIS gen. nov.

Name. An orthacean shaped like a saddle (Gk. ἀστράβη).

Diagnosis. Subcircular, biconvex, uniplicate shells with a deeply sulcate pedicle valve ornamented by coarse angular costellae ; ventral interarea curved apsacline with wide, open delthyrium ; dorsal interarea curved anacline with wide, open notothyrium ; shell probably impunctate.

Ventral interior with simple rounded teeth ankylosed to a pseudospondylium by solid deposits of secondary shell in adult valves, which may mask short receding dental plates, pedicle callist absent ; broad, medially divided adductor scars and

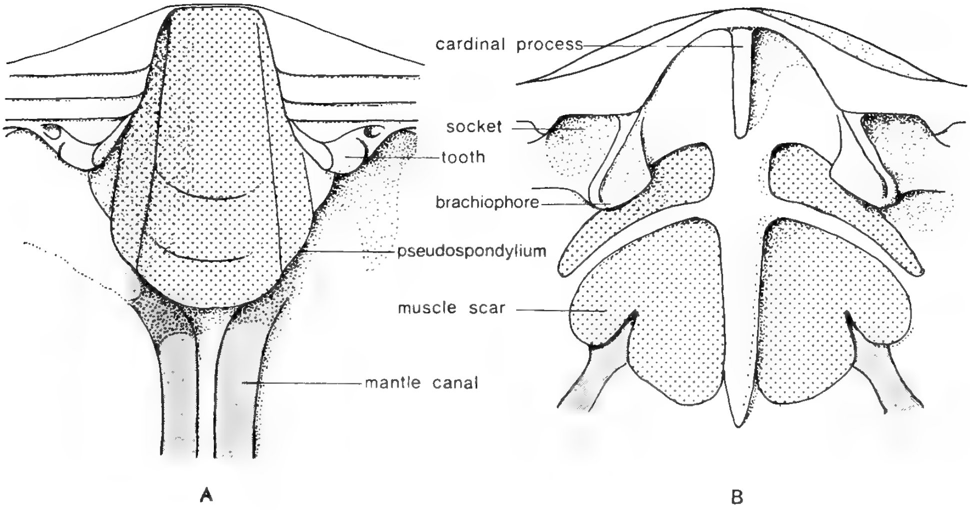


FIG. 6. Diagrammatic views of (A) the ventral and (B) the dorsal interiors of *Astraborthis*.

submedial lobes of diductor scars impressed on the floor of a strong pseudospondylium ; mantle canal pattern saccate.

Dorsal interior with a simple plate-like cardinal process and short, blade-like outward-curving brachiophores embedded in a thick deposit of secondary shell ; sockets oblique, notothyrial platform weak, fused with median ridge ; adductor scars quadripartite with smaller posterior pair ; mantle canal pattern probably digitate.

TYPE SPECIES. *Astraborthis uniplicata* sp. nov. from the Mytton Flags.

DISCUSSION. Although the new genus is obviously alimbellid in its general morphology, it differs from other members of the family in its ornament and certain aspects of its internal morphology. Externally it is immediately distinguishable from the smooth *Alimbella* and finely capillate *Medesia* in its coarse costellation and internally in the weak development of the notothyrial platform and the blade-like nature of the brachiophores. It further differs from *Alimbella* in its wide ventral adductor scar and from *Medesia* in the absence of branching and medial fusion of the proximal parts of the *vascula media*.

It may be of familial significance that dental plates have not yet been seen in adult pedicle valves of any of the three genera assigned to the Alimbellidae. It is, however, possible that short receding dental plates were developed during early growth stages but were later entirely buried in thick deposits of secondary shell secreted in the delthyrial cavity during formation of the pseudospondylium. Until young shells or their impressions have been examined it is safer to delay assessing the importance of this aspect of alimbellid morphology.

Astraborthis uniplicata gen. et sp. nov.

(Pl. 11, figs. 5, 6, 9, 11, 14; Text-fig. 6)

DIAGNOSIS. Subcircular, dorsibiconvex *Astraborthis* with the pedicle valve over four-fifths as long as wide and about one-third as deep as long; ventral sulcus rounded and about two-thirds as wide as the valve length, ornamented by angular costellae with a wavelength of about 1 mm, 10 mm anterior of the ventral umbo with 4 on the fold and up to 16 on the shell; pseudospondylium about one-third as long as the pedicle valve.

DESCRIPTION. Subcircular, strongly biconvex *Astraborthis* with the pedicle valve over four-fifths as long as wide and about one-third as deep as long; ventral sulcus flanked by evenly convex lateral slopes, rounded in profile, about two-thirds as wide as the length of the pedicle valve, projecting antero-dorsally to fit into rounded dorsal fold; brachial valve over one-third as deep as long, lateral slopes strongly and evenly convex; ventral interarea over one-quarter as long as the pedicle valve, dorsal interarea about one-eighth as long as the brachial valve, cardinal extremities obtusely rounded; radial ornamentation coarsely costellate with delayed costae originating at about 2 mm anterior of the umbo, with four occupying the crest of the fold, ribs sharply angular with a wavelength of about 1·0 mm at 10 mm anterior of ventral umbo.

Ventral interior with pseudospondylium elevated on a solid platform of secondary shell, about three-quarters as wide as long, lateral boundaries subparallel, anterior boundary rounded extending forward from the ventral umbo for one-third the length of the pedicle valve.

Dorsal interior with plate-like cardinal process obtusely triangular in lateral view, brachiophores short, curved, weakly divergent, adductor field strongly impressed divided by moderately strong median ridge and bounded posteriorly by weakly defined notothyrial platform.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	Incomplete external and internal moulds of pedicle valve (BB 35324a, b)	10·5	12·5
PARATYPE	Incomplete external and internal moulds of brachial valve (BB 35325a, b)	–	–

HORIZON AND LOCALITY. Mytton Flags exposed in small pathside quarry in the north-trending valley, 160 yds north-east of the north-east corner of Snailbeach Reservoir (Grid Ref. SJ 378024).

DISCUSSION. Only the incomplete moulds of a brachial and a pedicle valve, possibly the disarticulated remains of one shell, have so far been recovered from the Mytton Flags but the generic and specific individuality of the specimens cannot be doubted. Further collecting is desirable not only to assess the variation that occurred within the species but also to determine whether dental plates were developed in young specimens and to resolve the complete ribbing pattern, which, judged on the fragment of the dorsal exterior available at present, may have included about 16 costae, arising just anterior of the umbo.

Family **FINKELNBURGIIDAE** Schuchert & Cooper 1931

DIPARELASMA Ulrich & Cooper 1936

Diparelasma sp.

(Pl. 11, figs. 3, 7, 8)

The internal and an incomplete external mould of two brachial valves, 2 and 3 mm long respectively, and an incomplete external mould of a pedicle valve, collected from the Mytton Flags are best assigned to the finkelnburgiid *Diparelasma*. The moulds of one brachial valve and the pedicle valve (BB 35335a, b) came from a small exposure, 20 yds west of a runnel in the valley side north of the col separating Perkin's Beach and Mytton's Beach (Grid Ref. SJ 366002); those of the other brachial valve (BB 35336a, b) were obtained from outcrops near the top of the steep tributary to Crowsnest Dingle, 350 yds WNW of Blakemoorflat (Grid Ref. SJ 373008).

The moulds indicate that the shell was ventribiconvex and transversely subquadrate in outline with obtuse cardinal angles, had a sulcate brachial valve about 22% as deep as long and 64% as long as wide, and a pedicle valve about one-third as deep as long. Radial ornamentation was finely multicostellate with counts of 7 and 9 costellae per mm, 2 mm anterior of the umbones. The cardinalia consisted of blade-like brachiophores diverging from the anacline interarea with bases converging onto the floor of the valve on either side of a low median ridge to define a deep notothyrium containing a simple cardinal process. The fulcral plates were more strongly developed in the smaller valve as antero-lateral boundaries to the sockets. A pair of discrete adductor muscle scars extending anteriorly of the umbo for about half the length of the valve were impressed on either side of the median ridge.

Despite the lack of information about the ventral interior, the distinctive radial ornamentation and cardinalia leave little doubt that the moulds belong to *Diparelasma*. A number of species have been described from the Lower Ordovician, especially the Upper Canadian of N. America (Ulrich & Cooper 1938 : 147–156); but the cardinal process and dorsal sulcus are more strongly developed in the Shropshire specimens and may eventually prove to be diagnostic of a new species.

Family **PLECTORTHIDAE** Schuchert & Le Vene 1929

Subfamily **PLECTORTHINAE** Schuchert & Le Vene 1929

PLECTORTHIS Hall & Clarke 1892

Plectorthis whitteryensis sp. nov.

(Pl. 11, figs. 10, 13, 16, 17; Pl. 12, fig. 1)

DIAGNOSIS. Semi-elliptical, slightly ventribiconvex, rectimarginate *Plectorthis* with a pedicle valve 69% as long as wide and 22% as deep as long, ornamented by up to 27 costellae numbering 2 per mm, 5 mm antero-medially of the umbo, and bearing hollow embayments along the crests ; elongately oval ventral muscle scar extending forward for 28% of the length of the pedicle valve ; cardinal process ridge-like, simple.

DESCRIPTION. Semi-elliptical, subequally biconvex *Plectorthis*, 3 pedicle valves averaging 69% as long as wide (range 64% to 73%) and 22% as deep as long (range 21% to 24%) tending to become flatter away from the greatest depth of the valve in the umbonal region, and an evenly convex brachial valve with a mean depth relative to length of 19% (range 16% to 22%) for 3 valves ; anterior commissure rectimarginate, cardinal angles slightly obtuse ; radial ornamentation evenly costellate with up to 27 flat-crested, parallel-sided costellae numbering 2 per mm, 5 mm antero-medially of the umbo and arising by dichotomy of primary costae within 0·5 mm of the umbo, costellae becoming hollow at intervals of about 0·5 mm, interspaces finely striate and imbricate ; ventral interarea apsacline, delthyrium open, narrow, dorsal interarea shorter, anacline ; notothyrium open.

Ventral interior with elongately oval muscle field averaging 74% (range 63% to 93%) as wide as long and 28% (no range) as long as the length of the valve for 3 pedicle valves, with well-developed submedial diductor lobes meeting antero-medially to enclose a lanceolate undifferentiated adductor scar ; teeth small, supported by short subparallel to narrowly divergent dental plates extending anteriorly for an average of 9·5% the length of the valve for 2 valves.

Dorsal interior with a simple ridge-like cardinal process, brachiophores short, divergent, with bases slightly convergent to the floor of the valve and extending anteriorly for an average of 10% of the length for 3 valves ; short fulcral plates defining small suboval sockets, median ridge absent, adductor scars only rarely impressed as a pair of widely spaced bilobed scars extending anteriorly for about two-fifths the length of the brachial valve ; mantle canal systems unknown.

TYPE SPECIMENS.

		length	width (mm)
HOLOTYPE	External and internal moulds of pedicle valve (BB 35462a, b)	6·5	10·0
PARATYPES	External and internal moulds of brachial valve (BB 35463a, b)	5·0	–
	External and internal moulds of brachial valve (BB 35464a, b)	5·0	8·5
	External and internal moulds of pedicle valve (BB 37158a, b)	6·0	9·2

HORIZON AND LOCALITIES. Whittery Shales exposed in the lower part of the west bank of the River Camlad 60 yds north-east of Marrington Farm (Grid Ref. SO 272970).

DISCUSSION. Many Ordovician *Plectorthis* have been described, especially from North America (see Cooper 1956 : 447–456), but the species collected from the Whittery Shales is unique in the combination of a number of distinctive features, in particular the semi-elliptical outline and the peripheral flattening of the pedicle valve, the absence of a dorsal sulcus, the relative fineness of the costellate ornamentation, the variable development of a simple cardinal process and the occurrence of hollow embayments along the crests of the costae. Indeed, in respect of the last two features, the new species shows some affinity with *Desmorthis* Ulrich & Cooper 1936, and in view of the essential homogeneity of the American *Plectorthis* which suggests that they constitute a closely related species group, the Shropshire specimens may represent a stock with only remote ancestral links with their American contemporaries.

Plectorthis sp.

(Pl. 11, figs. 12, 15)

A complete internal mould and a fragment of the external mould (BB 35466a, b) of an orthacean pedicle valve, collected from Aldress Shales exposed in a bank of Ox Wood Dingle at the south-west corner of Ox Wood, a few yards north of the Rorrington–Wotherton road (Grid Ref. SJ 290007), have been provisionally identified as *Plectorthis*. The valve, which was about 13 mm long and 14·5 mm wide, was subcircular in outline with obtusely rounded cardinal angles and just over one-sixth as deep as long becoming flatter antero-medially. The surface was ornamented by microscopic concentric lamellae and 24 ribs which must have arisen at or near the umbo except for a few secondary costellae in the lateral areas. The ribs were rounded with a wavelength of 0·6 mm, 10 mm anterior of the umbo, and were separated by interspaces about 0·5 mm wide. The interarea was short, curved, and apsacline, the delthyrium open, and the small teeth were supported by widely divergent dental plates extending anteriorly for less than one-sixth the length of the valve. No identifiable muscle scars were impressed on the floor of the valve.

In the absence of impressions of the brachial valve, no valid comparisons can be drawn with described *Plectorthis*. The pedicle valve, however, is immediately distinguishable from that of *P. whitteryensis* sp. nov. in its subcircular rather than semi-elliptical outline, its significantly fewer ribs which are, moreover, rounded not flattened, and its widely divergent dental plates.

DESMORTHIS Ulrich & Cooper 1936

Desmorthis ? sp. nov.

(Pl. 12, figs. 2–4, 8)

Incomplete external and internal moulds of a brachial valve (BB 35337a, b), from exposures in a runnel to the east of the footpath to Blakemoorflat at the head of Mytton's Beach (Grid Ref. SJ 373006), are the sole representatives in the Mytton Flags of a highly distinctive plectorthid genus. The valve which was 7 mm long, semi-oval in outline, rectimarginate and gently convex medially with flattened lateral slopes, was ornamented by strong, sharply rounded hollow costellae numbering 2 per mm, 5 mm antero-medially of the umbo, and a subdued concentric ornamentation of faint lamellae. The planar anacline interarea was about one-tenth as long as the valve, the cardinal process a fine median ridge on a low notothyrial platform, separating two subtriangular diductor impressions. The short divergent brachiophores were pointed with low convergent bases bounding the notothyrial platform, while the narrow sockets were defined by well-developed fulcral plates. A linear median ridge extended anteriorly of the notothyrial platform for about two-fifths of the valve length, between suboval, poorly impressed adductor scars.

Two sets of external and internal moulds (BB 35338a, b ; BB 35339) from the Stapeley Volcanic Group collected from outcrops in an adit near Perkin's Beach, west of Shepherd's Rock, represent pedicle valves which appear to be conspecific with the brachial valve described above. The ornamentation, consisting of faint concentric lamellae and rather widely separated sharply rounded hollow costellae, is identical. Unfortunately little can be said about the internal morphology. In the larger specimen, which is 4 mm long, the ventral muscle field is not impressed and only the mould of a divergent dental plate, extending forward for about one-seventh the length of the mould, is seen.

The profiles of the valves, the development of hollow costellae and, with regard to the brachial valve from the Mytton Flags, the nature of the cardinalia are all indicative of the plectorthid affinities of the specimens. The simplicity of the cardinal process further suggests that the brachial valve, at least, is closer to *Desmorthis* than any other genus assigned to the family. However, the convergence of the brachiophores and the lamellose exterior hint that when the species is fully known it will prove to be generically distinct from other plectorthids.

GELIDORTHIS Havlíček

Gelidorthis cf. ***partita*** (Barrande)

(Pl. 12, figs. 5–7)

1879 *Orthis partita* Barrande : plate 63, fig. 11.
1950 *Giraldiella partita* (Barrande, 1879) Havlíček : 124.
1968 *Gelidorthis partita* (Barrande, 1879) Havlíček : 125.
1971 *Gelidorthis partita* (Barrande, 1879) Havlíček : 42.

A small number of impunctate valves never more than 8 mm long, from the Rorrington Beds exposed in Spy Wood Brook 20 yds downstream from where it joins Deadman's Dingle (Grid Ref. SO 289958), most closely compare with *Gelidorthis partita* (Barrande) from the Lower and Middle Caradoc rocks of Czechoslovakia. The shells were subquadrate in outline with an evenly convex pedicle valve (BB 37159 ; BB 35418a, b) about three-quarters as long as wide and about one-eighth as deep as long, and a very gently convex brachial valve (BB 35419a, b) lacking a definite sulcus. The relatively coarse radial ornamentation consists of angular costellae numbering 3 per mm at 5 mm antero-medially of the ventral umbo. The ribbing is strongly impressed internally even in the ventral umbonal cavity which is defined by short, widely divergent dental plates extending forward for about one-tenth the length of the pedicle valve. As in the pedicle valve, the dorsal muscle field is also obscured by internal ribbing ; but the cardinalia are well developed and consist of a cardinal process incipiently differentiated into a myophore and shaft, brachiophores supported by short convergent bases, and sockets defined by small fulcral plates.

These features are consistent with the variability described by Havlíček (1950 : 124 ; 1971 : 42) in young specimens of *G. partita*, although the brachial valve of the Shropshire *Gelidorthis* appears to be relatively flatter. However only two of these valves are known at present and until more material including adult specimens is available for the significance of this difference to be assessed, there is no justification in according them systematic recognition.

TAZZARINIA Havlíček 1971

Tazzarinia elongata sp. nov.

(Pl. 12, figs. 9–12, 15)

DIAGNOSIS. Elongately subquadrate, ventribiconvex *Tazzarinia* with a coarsely fascicostellate ornamentation and a dorsal sulcus dying out anteriorly ; bilobed ventral muscle scar extending forward for almost 30% the length of the pedicle valve ; pointed brachiophores supported by short bases.

DESCRIPTION. Subquadrate, ventribiconvex *Tazzarinia* with slightly obtuse cardinal angles ; pedicle valve almost as long as wide and one-quarter as deep as long, slightly carinate medially with evenly convex lateral slopes ; brachial valve about four-fifths as long as wide and one-sixth as deep as long, with a narrow median sulcus becoming indistinct beyond the 4 mm growth stage, lateral slopes evenly convex ; radial ornamentation strongly fascicostellate with narrowly rounded costellae numbering 5 per mm, 3·5 mm antero-medially of the dorsal umbo ; ventral interarea slightly curved apsacline, longer than the anacline dorsal interarea, notothyrium and delthyrium open but pedicle callist strongly developed within the latter.

Teeth supported by narrowly divergent dental plates extending forward for about one-sixth the length of the pedicle valve ; ventral muscle scar strongly bilobed with a median adductor track and flanking diductors impressed anteriorly for almost three-tenths the length of the valve.

Cardinal process massive with crenulated posterior face, notothyrial platform well developed passing anteriorly into median ridge and flanked by convergent bases of pointed brachiophores, sockets elongate with small fulcral plates ; suboval adductor scars impressed on either side of median ridge and extending anteriorly for over two-fifths the length of the brachial valve.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	External and internal moulds of brachial valve (BB 35332a, b)	5·5	–
PARATYPE	External and internal moulds of pedicle valve (BB 35333a, b)	3·8	3·8

Type horizon and locality. Meadowtown Beds exposed in a small excavation in the corner of a field alongside the cart-track from Meadowtown to Waitchley, 330 yds south of Waitchley (Grid Ref. SJ 311017).

Discussion. Although the moulds of only one pedicle and one brachial valve of *Tazzarinia* have been recovered from the Meadowtown Beds, there is no doubt about their generic affiliations or their specific distinctiveness. The specimens compare in every important respect with the *Tazzarinia* described by Havlíček (1971 : 39) from the Lower Caradoc of Morocco except that bilobation of the cardinal process cannot be confirmed in the Shropshire dorsal mould. Yet the Shelve form is immediately distinguishable from both Moroccan species, *T. drotae* and *T. foraminosa*, especially in its coarsely fascicostellate ornamentation and its elongately subquadrate outline.

Subfamily **PLATYSTROPHIINAE** Schuchert & Le Vene 1929

PLATYSTROPHIA King 1850

Platystrophia caelata sp. nov.

(Pl. 12, figs. 13, 14, 16–19)

Diagnosis. Subquadrate, dorsibiconvex *Platystrophia* with the pedicle valve 76% as long as wide and 32% as deep as long, with a flat-bottomed sulcus 54% as wide as the valve length, ornamented by 2 costae in the sulcus and 10 to 14 on the lateral slopes with lamellae extending along the crests of costae as short rounded canopies.

Description. Subquadrate, dorsibiconvex, uniplicate *Platystrophia* with subrectangular cardinal angles, the brachial valve just over two-fifths as deep as long, the pedicle valve on average 76% (range 70% to 79%) as long as wide and 32% (range 28% to 35%) as deep as long for 3 valves, with a flat-bottomed sulcus with a mean width of 54% (range 50% to 57%) relative to the length for 3 valves, and evenly convex lateral slopes ; dorsal interarea short, anacline, ventral interarea curved, apsacline about one-fifth as long as pedicle valve ; costae angular with a wavelength of just over 1 mm, 5 mm anterior of dorsal umbo, covered with densely distributed tubercles and numbering 2 in the ventral sulcus with 10 to 14 on the lateral slopes ; lamellae strongly developed and, beyond 4 mm from umbones, extending along the crests of the costae as short, rounded canopies partially covering subtriangular concave pads of secondary shell.

Ventral interior with small pedicle callist, thick teeth supported by short, receding dental plates extending anteriorly for less than one-fifth the length of the pedicle valve, and subtriangular muscle field with wide adductor impressions occupying the floor of the valve, less than half as wide as long and extending anteriorly for just over two-fifths the length of the pedicle valve ; mantle canal impressions obscure but ventral system possibly digitate with abbreviated *vascula media* occupying the crests of the costae in the sulcus and gonocoels spreading antero-laterally along the crests of the lateral costae.

Dorsal interior with ridge-like cardinal process and wide notothyrium bounded by secondarily thickened short brachiophores extending anteriorly for about one-fifth the length of the brachial valve ; dorsal adductor impressions quadripartite, extending anteriorly for almost half the length of the brachial valve on either side of a low median ridge with the subtriangular anterior pair the larger.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	External and internal moulds of brachial valve (BB 35493a, b)	9·5	–
PARATYPES	External and internal moulds of pedicle valve (BB 35494a, b)	9·0	11·7
	External and internal moulds of pedicle valve (BB 35495a, b)	10·5	15·0

HORIZON AND LOCALITIES. Whittery Shales : BB 35493 from Whittery Quarry at the south end of Whittery Wood, near Chirbury (Grid Ref. SO 275981) ; BB 35494, BB 35495 from exposures in the lower part of the west bank of the River Camlad, 60 yds north-east of Marrington Farm (Grid Ref. SO 272970).

DISCUSSION. The *Platystrophia* which occurs rarely in the Whittery Shales has a highly distinctive concentric ornamentation of differentially developed lamellae. Most *Platystrophia* are variably lamellose and some such as *P. chama* Eichwald (as figured by Alichova 1953 : 131) strikingly so, but in *P. caelata* sp. nov. more than 4 mm long strong lamellae occur at regular intervals of about 0·5 mm and their forward growth along the costae was accompanied by an equally regular sag of the mantle edge. The resultant pattern is a series of subcircular, narrow canopies, aligned along the crests of the costae, inclined at about 35° to the shell surface and overhanging the posterior parts of alternating, depressed, subtriangular areas of secondary shell. In the intercostate spaces, the lamellae lie flat on one another as a series of overlapping tongues directed anteriorly. This ornament is characteristic of all eight specimens of the genus collected from the Whittery Shales. It is unknown in any other described *Platystrophia*, and in recognition of its uniqueness a new species has been erected to include the Whittery shells.

In other features, the new species appears to be unexceptional, although this may be due to the meagreness of the sample. Judging from the clarity of gonadal impressions and muscle scars which are deeply inserted even on the notothyrial floor and about the cardinal process, specimens attaining a length of 10 mm were gerontic individuals so that at least the Whittery representatives of the species were small in size. All specimens showing the disposition of the costae on the fold and sulcus were biplicate. The interiors of both valves show less secondary thickening than is typical of later species of *Platystrophia*, but, even so, the brachiophore bases in the brachial valve are heavily encased in secondary shell as are the ventral umbonal chambers.

Platystrophia cf. ***major*** Williams 1955

(Pl. 13, figs. 1, 2, 4)

1955 *Platystrophia precedens* McEwan *major* Williams : 402.

The moulds of two immature valves of *Platystrophia* lacking the distinctive concentric ornamentation of *P. caelata* sp. nov. have also been found in the Shelve area. They are the moulds of a brachial valve nearly 5 mm long (BB 35586a, b) from Aldress Shales exposed in the bank of Ox Wood Dingle at the south-west corner of Ox Wood a few yards north of the Rorrington–Wotherton road (Grid Ref. SJ 290007), and a pedicle valve 5·5 mm long (BB 35587a, b) from the Spy Wood Grit exposed on top of the ridge 1440 yds NNE of the Rorrington bench mark 599 (Grid Ref. SJ 303018). Neither valve can be completely reconstructed from the indifferently preserved moulds but the brachial valve appears to have been about 80% as long as wide and 20% as deep as long with a well-defined rounded fold about 40% as wide as the valve. The radial ornamentation consists of 3 costae on the fold and 5 on each lateral slope with a wavelength of 0·7 mm, 5 mm antero-medially of the umbo. Only impressions of subparallel brachiophore bases and a blade-like cardinal process are preserved internally. The pedicle valve was similarly ornamented, although traces of fine concentric lamellae are also sporadically preserved, while internally the ventral muscle scar extended well beyond the slightly divergent dental plates for 36% of the valve length.

These few statistics and especially the presence of 3 costae on the fold and 2 in the sulcus suggest that both valves may be provisionally assigned to *P. major* Williams (in Whittington & Williams 1955 : 402) first described from the Derfel Limestone of N. Wales. The species is morphologically like the American species *P. precedens* McEwan but is now also known from the Upper Llandeilo (MacGregor 1961 : 184). New evidence on intraspecific variability in the arrangement of costae suggests that the species is more likely to be related to the *Platystrophia dentata* (Pander) group from the Baltic (Williams 1963 : 371).

MCEWANELLA Foerste 1920

Mcewanella sp.

(Pl. 13, figs. 3, 5)

An incomplete pedicle valve (BB 35416) and a deformed internal ventral mould (BB 35417) from the Whittery Shales exposed in the stream at the north end of Spring Coppice 865 yds south-east of Hockleton Bridge (Grid Ref. SO 279997) are the only specimens of *Mcewanella* so far recovered in the Shelve area.

Growth lines on the valve which was about half as deep as long, and shallowly sulcate antero-medially, indicate that the outline changed from semi-circular to subquadrate during growth, because the immature valve was widest along the mucronate hinge-line whereas fully developed valves were about as wide as long with the maximum width well anterior of the hinge line with its orthogonal cardinal angles. The external surface was ornamented by branching costellae numbering

3 per mm, 5 mm antero-medially of the umbo and further corrugated by up to 7 radiating rounded costae with a wavelength of about 3 mm, 10 mm antero-medially of the umbo.

The ventral mould is distorted umbonally but there is evidence of an apsacline interarea and massive trigonal teeth supported by strong, narrowly divergent dental plates. The ventral muscle scar was elongately oval with a broad median adductor track reaching to the anterior margin.

The specimens are closely related to the Upper Llandeilo *M. berwynensis* (MacGregor 1961 : 183). However, the Welsh *Mcewanella* bears a ventral fold, and 9 superimposed costae, and until the variability of these features can be ascertained in the Shropshire form it seems safer to withhold specific identification.

SALACORTHIS gen. nov.

Name. An orthacean with an external ornament like a sieve (Gk. σάλαξ).

Diagnosis. Subquadrate, biconvex, uniplicate shells with a strong dorsal median fold emerging from a neanic sulcus and a complementary ventral sulcus ; radial ornamentation coarsely costate to costellate with two or three thick rounded costae on the fold and up to three equally wide costae on each lateral slope, costellae arising sporadically in later growth stages either by division of costae or as intercalations in the interspaces ; external shell surface also ornamented by densely distributed, deep exopuncta arranged quincuncially ; ventral interarea curved, apsacline with open triangular delthyrium, dorsal interarea shorter, slightly curved anacline, notothyrium open ; shell impunctate.

Ventral interior with strong teeth supported by short but well-defined dental plates extended on the valve floor as raised ridges laterally bounding an elongately oval undifferentiated muscle field ; ventral mantle canal system unknown.

Dorsal interior with a wide notothyrial platform bearing a median ridge-like cardinal process, brachiophores rod-like, divergent, continuous laterally with strong concave fulcral plates defining oblique, hemiconical sockets ; brachiophore bases large, convergent onto notothyrial platform and median ridge ; dorsal adductor scars divided by median ridge into a pair of triangular undifferentiated impressions with the apices directed posteriorly and deeply inserted beneath the anterior borders of the brachiophore bases ; dorsal mantle canal system unknown.

Type species. *Salacorthis costellata* sp. nov. from the Spy Wood Grit.

Discussion. The new genus, with the exception of a poorly preserved exfoliated pedicle valve revealing the impunctate nature of the shell, is represented solely by a few moulds from the Spy Wood Grit. Yet its affinities are not in doubt because it combines the typical cardinalia of the Plectorthidae with the coarsely costate ornamentation and strongly uniplicate anterior margin of the Platystrophinae. Indeed with regard to its radial ornamentation it anticipates the relationship between *Platystrophia* and *Mcewanella* (Schuchert & Cooper 1932 : 69). The former is costate and the latter is believed, at least in respect of the American species, to have been derived from *Platystrophia* by the superimposition of a multicostellate ornament. The beginnings of a similar development can be seen in one external mould of *Salacorthis* (Pl. 13, fig. 12) but it was not necessarily typical of the species because no costellae were developed in a larger pedicle valve and even in the figured specimen costellae did not appear until the valve was about 7 mm long. The new genus therefore differs from both *Platystrophia* and *Mcewanella* in being sporadically costellate.

The principal difference, however, and one which immediately distinguishes *Salacorthis* from the other two members of the Platystrophinae, lies in the conspicuously exopunctate appearance of the shell surface. The exopuncta were deep coarse pits penetrating the external shell vertically for depths of about 0·1 mm and arranged in a closely crowded quincuncial pattern. They are quite different in morphology and origin from the obliquely disposed apertures which constitute the 'hollow ribs' so typical of the plectorthids (Williams in Williams *et al.* 1965 : H70), and are all the more unexpected because the external surface of *Platystrophia* is noteworthy among orthaceans for being distinctively pustulose.

Internal characters that indicate the platystrophiinid affinities of *Salacorthis* include the simple cardinal process and the suboval ventral field which, although undifferentiated in known specimens of the new genus, probably consisted of a broad adductor scar flanked by elongate bases for the diductors and adjustors, as in *Platystrophia*. The brachiophores and their supporting bases are also comparable, although the degree to which the posterior parts of the dorsal adductor impressions are inserted behind the brachiophore bases of *Salacorthis* is unmatched in *Platystrophia* and *Mcewanella*. But such internal differences as exist are minor and do not affect the conclusion that *Salacorthis* arose out of the earlier established *Platystrophia*.

Salacorthis costellata gen. et sp. nov.

(Pl. 13, figs. 6–13 ; Text-fig. 7)

DIAGNOSIS. Dorsibiconvex, subquadrate *Salacorthis* with a brachial valve about three-quarters as long as wide and 37% as deep as long ; dorsal fold almost half as wide as valve length, bearing 2 or 3 costae with a wavelength of 1·5 mm, 5 mm antero-medially of the umbo, with 2 or 3 on the flanks, all becoming costellate in late growth stages ; ventral muscle scar suboval extending forward for nearly one-third the length of the pedicle valve ; dorsal median septum short.

DESCRIPTION. Dorsibiconvex, subquadrate *Salacorthis* with cardinal angles becoming obtuse in adult growth stages, pedicle valve about one-quarter as deep as long, brachial valve three-quarters as long as wide with a mean depth relative to length of 37% for 3 brachial valves ; dorsal fold 49% as wide as the length of 3 brachial valves bearing 2 or 3 strong costae with a wavelength of about 1·5 mm, 5 mm antero-medially of the dorsal umbo, with 2 or 3 additional costae on each of the lateral slopes, all costae may split into costellae in late growth stages ; exopuncta coarse with counts of 3 per 0·5 mm, 5 mm anterior of the umbo.

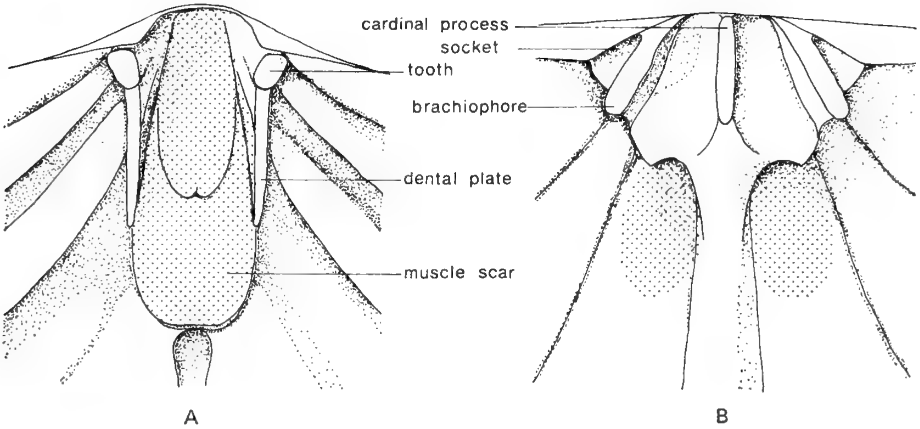


FIG. 7. Diagrammatic views of (A) the ventral and (B) the dorsal interiors of *Salacorthis*.

Ventral interior with subparallel dental plates extending forward for one-seventh the pedicle valve length, suboval ventral muscle scar undifferentiated, extending anteriorly for nearly one-third the length of the pedicle valve.

Dorsal interior with brachiophore bases extending forward for over one-quarter the length of the brachial valve; median septum supporting the cardinalia short, extending anteriorly for two-fifths the length of the brachial valve.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	External and internal moulds of brachial valve (BB 37153a, b)	3·7	5·0
PARATYPES	Internal mould of pedicle valve (BB 37154)	11·0	12·0
	Incomplete external mould of brachial valve (BB 37155)	–	–
	Incomplete external mould of brachial valve (BB 37156)	–	–
	Incomplete external mould of brachial valve (BB 37157)	4·5	–

HORIZON AND LOCALITIES. Spy Wood Grit: BB 37153, 37154 from exposures on top of ridge 1440 yds NNE of Rorrington bench mark 599 (Grid Ref. SJ 303018); BB 37155, 37157 from outcrops 1100 yds NNE of Rorrington (Grid Ref. SJ 303015); BB 37156 from outcrops in the north bank of Spy Wood Brook 170 yds north-east of Spy Wood Cottage (Grid Ref. SO 282958).

DISCUSSION. No other species congeneric with *Salacorthis costellata* has yet been so described although in view of the strongly developed platystrophiinid characters of the Spy Wood form and the microscopic nature of its chief differentiating feature, some stocks, currently recorded as *Platystrophia* or *Mcewanella*, may ultimately prove to belong to the genus.

Family **SKENIDIIDAE** Kozlowski 1929

Genus ***SKENIDIOIDES*** Schuchert & Cooper 1931

Skenidioides cf. ***costatus*** Cooper

(Pl. 13, figs. 14–16 ; Pl. 14, figs. 1–3)

1956 *Skenidioides costatus* Cooper : 493.
1963 *Skenidioides* cf. *costatus* Cooper ; Williams : 375.

Diagnosis. Subpyramidal, ventribiconvex *Skenidioides* with a carinate pedicle valve 54% as long as wide and 55% as deep as long, ornamented by up to 8 costae on each of the lateral slopes and a thick median costa giving rise to a pair of lateral costellae 1·5 mm anterior of the umbo.

Description. Semi-oval, sulcate *Skenidioides* with a subpyramidal, carinate pedicle valve with a mean length relative to width of 54% (range 50% to 59%) for 4 valves and a mean depth relative to length of 55% (range 53% to 58%) for 3 valves ; brachial valve very gently convex with a sharp median sulcus ; radial ornamentation costate with up to 8 rounded costae occupying each lateral slope but with ventral carina defined by thick rounded costa, about 0·5 mm in wavelength 2 mm anterior of ventral umbo, giving rise to a pair of lateral costellae about 1·5 mm anterior of ventral umbo.

Ventral interior with free spondylium about one-fifth as deep as the length of the valve.

Dorsal interior with thin and plate-like cardinal process continuous with high median septum, brachiophore bases converging onto dorsal septum at an average of 33% the length of 2 brachial valves ; dorsal adductor field as a pair of subtriangular impressions divided by median septum and extending anteriorly for nearly three-fifths the length of the brachial valve.

Figured material.

	length	width (mm)
Internal mould of brachial valve (BB 35409)	2·3	4·4
Incomplete internal mould of pedicle valve (BB 35410)	2·5	4·4
Internal mould of pedicle valve (BB 35411)	1·2	2·7
Internal mould of pedicle valve (BB 35412)	0·8	1·5
Incomplete external mould of pedicle valve (BB 35413)	1·5	–

Horizons and localities. Spy Wood Grit : BB 35411 to 35413 from exposures in north bank of Spy Wood Brook, 170 yds north-east of Spy Wood Cottage (Grid Ref. SO 282958). Whittery Shales : BB 35409 from exposures in the lower part of the west bank of the River Camlad, 60 yds north-east of Marrington Farm (Grid Ref. SO 272970) ; BB 35410 from exposures in the stream at the north end of Spring Coppice, 865 yds south-east of Hickleton Bridge (Grid Ref. SO 279997).

Discussion. Moulds of *Skenidioides* occur only rarely in both the Spy Wood Grit and Whittery Shales but are clearly related to the species found in the Gelli-grin

Calcareous Ashes which has been compared with S. *costatus* Cooper from the Porterfield of North America (Williams 1963 : 375). In internal proportions and the shape of the shell the likeness is certainly close and, although the Shelve pedicle valve tended to be relatively wider and deeper than the average Bala one, the differences are not important. Indeed the only indication of a difference which may eventually prove to be important is in the lack of development of a costellate ornamentation on the Shelve *Skenidioides*. The sample is indistinguishable from S. *costatus* in the number and wavelength of costae, but only the ventral median costa of the Shelve specimens gave rise to costellae, whereas external branches arose freely from the lateral costae of the Bala stock. This difference is not entirely related to the overall greater size attained by the Bala shells. Within the size range of the Shelve specimens, which are between 0·8 and 2·0 mm long, costellae branched from one or more lateral costae in 7 out of 12 pedicle valves from the Gelli-grin Group. It is therefore possible that the Shelve *Skenidioides* were characterized by a simplicity of ribbing that persisted throughout growth, but larger collections will have to be obtained to determine whether taxonomic recognition of the difference is worth while.

PROTOSKENIDIOIDES gen. nov.

NAME. One of the first skenidiids.

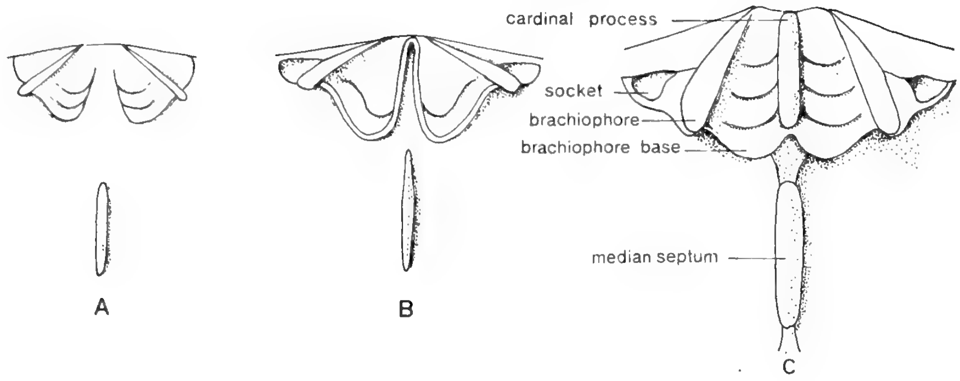
DIAGNOSIS. Transversely semi-oval, plano-convex shells with a high carinate pedicle valve and sharply sulcate brachial valve ; radial ornamentation costate with a wide ventral median costa forming the carina of the pedicle valve and corresponding to the dorsal sulcus ; ventral interarea long, planar, apsacline with an open delthyrium, dorsal interarea shorter, planar, anacline ; shell probably impunctate.

Ventral interior with pointed teeth and shallow spondylium apparently free of the valve floor ; muscle and mantle canal impressions unknown.

Dorsal interior with divergent brachiophores supported by flat-lying brachiophore bases, discrete and transversely lobate in young shells but extending anteriorly as elevated plates in adult shells and converging medially to form a ridge-like cardinal process which is joined by a low swelling on the valve floor with a high long median septum ; sockets narrow oblique, defined by concave elevated fulcral plates in adult shells only ; adductor muscle field divided by median septum into two elongated oval impressions bounded laterally by raised curved ridges ; dorsal mantle canal system unknown.

TYPE SPECIES. *Protoskenidioides revelata* sp. nov. from the Mytton Flags.

DISCUSSION. The skenidiid found in the Mytton Flags is represented exclusively by fragile moulds of what must have been thin-shelled valves, but although the smallest impression of the brachial valve recovered is about 4 times as long as that of the protegulum, the size range (0·8 mm to 2·0 mm in valve length) is sufficiently great to reveal some hitherto unsuspected aspects of the origin and development of the skenidiid cardinalia.



length (mm)	A	B	C
0–0·9	5	1	
1·0–1·4		2	
1·5–2·0		1	4

FIG. 8. Diagrammatic views of the dorsal interiors of *Protoskenidioides* showing three stages (A, B, C) in the development of the cardinalia during ontogeny; with a correlation table below indicating the relationship between the length of the brachial valve and the illustrated growth stages of the cardinalia.

The smallest moulds show that when brachial valves were less than 1 mm long the brachiophores were well developed and widely divergent (Text-fig. 8). Posterolaterally they were flanked by simple slot-like sockets indented on the valve floor. Antero-medially they were continuous with a pair of transversely oval areas defined by slightly elevated anterior boundaries that converged towards the notothyrial apex of the valve. It is assumed that these wide, discrete areas represented the seats for the attachment of the dorsal ends of the diductor muscles rather than supports for the brachiophores although it is convenient to refer to them as brachiophore bases. At this growth stage there was no notothyrial platform and the valve interior was dominated by the median elevation representing the external sulcus bearing a small, thin, median septum.

With further growth the antero-lateral parts of the sockets were raised above the valve floor by the development of concave fulcral plates and the brachiophore bases were extended anteriorly as a pair of lobate platforms which were also free of the valve floor. The bases also encroached onto the median elevation which bore a small ridge in some valves, finally to converge and form a simple cardinal process clearly made up of the adjacent borders of the brachiophore bases and contained within a low, anteriorly bilobed septalium. Concomitantly the median septum extended anteriorly and also posteriorly almost to unite with the cardinal process from which it was separated by a low saddle representing a remnant of the median elevation.

These modifications leading to the definition of the septalium are unknown in younger skenidiids and serve to distinguish *Protoskenidioides* from other members of the family. In *S.* cf. *costatus* Cooper from the Gelli-grin Group, for example, impressions of the smallest brachial valves known, which are just over 1 mm long, show that the septalium was not bilobed but evenly convex anteriorly as in adult valves, and that it contained a high cardinal process not yet differentiated into a myophore and shaft but which was continuous with the median septum and bore no sign of having been built up from the median edges of the brachiophore bases.

The likelihood that *Protoskenidioides* gave rise to *Skenidioides* by an accelerated development of a well-defined septalium is strengthened by the close comparison between the two genera in other characteristics such as the distinctive shape and ornamentation. Even the inference that the spondylium in the pedicle valve of *Protoskenidioides* is free does not militate against the relationship because a septal support to the spondylium of *Skenidioides* cannot always be identified without recourse to apical sections of the shell. Such a line of descent is also still consistent with the suggestion (Kozlowski 1929 : 129) that the skenidiids were derived from the finkelnburgiids : indeed the attitude of the slightly inclined, convergent brachiophore bases of *Protoskenidioides* is more reminiscent of *Finkelnburgia* than the later skenidiids.

Protoskenidioides revelata gen. et sp. nov.

(Pl. 14, figs. 4–13 ; Text-fig. 8)

Diagnosis. Subpyramidal, mucronate *Protoskenidioides* with a planar brachial valve 47% as long as wide, lateral slopes ornamented by up to 18 costae with a broad ventral median costa corresponding to a dorsal sulcus 0·4 mm wide, 1·5 mm antero-medially of the umbo.

Description. Transversely semi-oval, mucronate *Protoskenidioides* with a subpyramidal pedicle valve and a planar brachial valve averaging 47% (range 45% to 48%) as long as wide for 4 valves with a well-defined rounded median sulcus consistently 0·4 mm wide, 1·5 mm antero-medially of the umbo of 4 valves ; radial ornamentation on lateral slopes consisting of up to 18 costae increasing in number during growth by implantation with the right lateral consistently 0·2 mm wide in 4 valves, and the ventral median costa complementary to the dorsal sulcus about 0·6 mm wide in adult shells.

Ventral interior with shallow spondylium, broadly convex anteriorly.

In adult brachial valves the septalium, about half as long as wide, extended anteriorly for an average of 23% (range 21% to 26%) the length of 5 valves but it was not continuous with a long median septum which may have reached the anterior margin, adductor muscle field extending anterior of dorsal umbo for almost three-quarters the length of the valve.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	Internal mould of brachial valve (BB 35387)	1·7	3·0
PARATYPES	External and internal moulds of brachial valve (BB 35388a, b)	1·3	2·6
	Incomplete internal mould of pedicle valve (BB 35389)	–	–
	Incomplete internal mould of brachial valve (BB 35390)	1·2	–
	Incomplete external mould of brachial valve (BB 35391)	–	–
	Incomplete internal mould of brachial valve (BB 35392)	0·8	–
	Incomplete internal mould of brachial valve (BB 35393)	1·1	–
	External and internal moulds of brachial valve (BB 35394a, b)	1·6	–
	External and internal moulds of pedicle valve (BB 35395a, b)	1·1	2·0
	Internal mould of brachial valve (BB 35396)	1·9	–
	External and internal moulds of brachial valve (BB 35397a, b)	1·6	–
	External and internal moulds of brachial valve (BB 35398a, b)	1·5	–
	External and internal moulds of brachial valve (BB 35399a, b)	1·7	–
	External and internal moulds of brachial valve (BB 35400a, b)	2·0	–
	External and internal moulds of brachial valve (BB 35401a, b)	0·9	1·7

HORIZON AND LOCALITIES. Mytton Flags: BB 35387 to 35393, BB 35398, 35399 from a trench excavated in Shelve Church Beds (Grid Ref. SO 335990); BB 35394 to 35397 from exposures of Shelve Church Beds along a cart-track near Wood House, Gravels (Grid Ref. SJ 338003); BB 35400, 35401 from Shelve Church Beds exposed along a cart-track 50 yds north-west of Wood House, near Gravels (Grid Ref. SJ 337002).

DISCUSSION. The moulds of the new species that have been collected are so closely crowded and so commonly collapsed that only a few statistical data were obtainable to indicate the variability of the new species. These are included in the description given above.

Superfamily **ENTELETACEA** Waagen 1884

Family **SCHIZOPHORIIDAE** Schuchert & Le Vene 1929

Subfamily **DRABOVIINAE** Havlíček 1950

DRABOVIA Havlíček 1950

Drabovia cf. ***fascicostata*** Havlíček

(Pl. 14, figs. 14–16, 18, 19)

1950 *Drabovia fascicostata* Havlíček : 15.
1950 *Drabovia fascicostatata* Havlíček : 47.
1950 *Drabovia fascicostata* Havlíček : 47.

Diagnosis. Ventribiconvex *Drabovia* ornamented by fascicostellae with about 5 ribs per mm, 5 mm antero-medially of dorsal umbo.

Description. Semi-elliptical, ventribiconvex, sulcate *Drabovia*, with orthogonal cardinal angles of young shells becoming obtuse in mature growth stages so that the hinge line is less than the maximum width of the shell ; carinate pedicle valve 33% as deep as long, brachial valve 73% as long as wide and 15% as deep as long (the mean for 4 valves) with an evenly concave sulcus and evenly convex sides ; ventral interarea relatively short, curved apsacline, dorsal interarea very short anacline, delthyrium and notothyrium open ; radial ornamentation fascicostellate, divided into sectors by capillae, with counts of 6 and 5 ribs per mm occurring 5 mm antero-medially of the umbones of 1 and 4 brachial valves respectively, costellae branching internally in valves up to 5 mm long with 1ā, 2ā, 3ā and 4ā occurring early but with 3a°)3ā1̄ā, 3a°)3c̄ and 4a°)4b̄ present (costellae insertion code of Bancroft, 1945).

Cardinal process with a very small bulbous myophore and relatively long linear shaft, becoming thicker in mature valves, continuous with median ridge-like posterior part of sulcus ; brachiophores short, acutely divergent, bases 17% as long as the brachial valve, parallel or convergent with the median ridge, sockets rarely defined by fulcral plates ; muscle scar unknown.

Teeth small supported by slightly divergent dental plates extending forward for 16% the length of the pedicle valve ; ventral muscle field subcordate with broad adductor scar bounded laterally by lobate diductor scars impressed anteriorly for about one-quarter the pedicle valve length.

Figured material.

	length	width (mm)
External and internal moulds of brachial valve (BB 35316a, b)	4·0	4·8
External and internal moulds of brachial valve (BB 35317a, b)	4·5	9·4
External and internal moulds of pedicle valve (BB 35318a, b)	4·5	5·2
External and internal moulds of pedicle valve (BB 35319a, b)	5·5	7·5

Horizon and locality. Spy Wood Grit exposed 1100 yds NNE of Rorrington (Grid Ref. SJ 303015).

DISCUSSION. The first *Drabovia* recorded in the British Isles is represented by a small number of moulds (Tables 51–54) which compare closely with *D. fascicostata* Havlíček (1950 : 47) from the Caradocian Letná Beds of Czechoslovakia. The ribbing of the Shropshire specimens may prove to be finer and the pedicle valve more convex but, provisionally at least, these differences are less important than the many points of resemblance.

TABLE 51

Statistics of length (l) and maximum width (w) of 17 brachial valves of *Drabovia* cf. *fascicostata* Havlíček

$\bar{l}$ mm (var l)	2·71 (1·192)
$\bar{w}$ mm (var w)	3·71 (1·361)
r	0·956
a (var a)	1·1068 (0·00647)

TABLE 52

Statistics of length (l) and maximum depth (th) of 7 pedicle valves of *Drabovia* cf. *fascicostata* Havlíček

$\bar{l}$ mm (var l)	3·21 (1·231)
$\overline{th}$ mm (var th)	1·06 (0·069)
r	0·988
a (var a)	0·2375 (0·00028)

TABLE 53

Statistics of length (l) of 8 pedicle valves and the length of dental plates (dl) of *Drabovia* cf. *fascicostata* Havlíček

$\bar{l}$ mm (var l)	3·47 (0·931)
$\overline{dl}$ mm (var dl)	0·57 (0·043)
r	0·837
a (var a)	0·2161 (0·00233)

TABLE 54

Statistics of length (l) and the length of brachiophore bases (lc) in 8 brachial valves of *Drabovia* cf. *fascicostata* Havlíček.

$\bar{l}$ mm (var l)	3·52 (0·831)
$\overline{lc}$ mm (var lc)	0·59 (0·015)
r	0·820
a (var a)	0·1367 (0·00102)

NOCTURNIELLA Havlíček 1950

Nocturniella sp.

(Pl. 14, figs. 17, 20)

The internal mould (BB 35341) of a brachial valve, about 4 mm long and 4·5 mm wide, is the only draboviinid so far recovered from the Mytton Flags –70 yds north of the entrance to Yewtree Level, The Hollies, Snailbeach (Grid Ref. SJ 380018). The valve was subcircular in outline and about one-sixth as deep as long with evenly convex lateral areas and a strong median sulcus, represented by a broad median ridge on the valve interior, becoming fainter anteriorly. Internal impressions of ribbing indicate that the valve tended to be multicostellate with 5 costellae per mm at the antero-medial margin. The short planar interarea is anacline, divided medially by a notothyrium with a low platform bearing a linear cardinal process, and bounded by short pointed brachiophores with subparallel bases extending forward for one-eighth the length of the valve and sockets defined by fulcral plates. The adductor muscle scar impressions are faint and incomplete.

In the absence of impressions of the pedicle valve, identification of the specimen is not a certainty. However, the presence of a sulcus and the subparallel attitude of the brachiophore bases favour its assignment to *Nocturniella*. Yet it is quite distinct from the only described species of that genus, *N. nocturna* Barrande from the Arenig Komarov Beds of Czechoslovakia (Havlíček 1950 : 125), especially in the plate-like aspect of its cardinal process and the anterior suppression of the sulcus.

Family **DALMANELLIDAE** Schuchert 1913

DALMANELLA Hall & Clarke 1892

Dalmanella parva Williams emended

(Pl. 15, figs. 1–4, 7)

1949 *Dalmanella parva* Williams : 169.

Diagnosis. Small, ventribiconvex *Dalmanella* with a brachial valve 77% as long as wide, and with fine costellae, rarely branching externally, numbering about 6 per mm at the 2 mm growth stage ; dental plates 23% as long as the pedicle valve and 130% as divergent as long ; subparallel brachiophore bases 22% as long as the brachial valve and separated from each other by 97% of their length.

Description. Small, ventribiconvex *Dalmanella* with obtuse cardinal angles ; pedicle valve 32% as deep as long with a carinate rounded median zone and evenly sloping lateral areas ; brachial valve 77% as long as wide and about one-fifth as deep as long with a shallow median sulcus almost three-quarters as wide as valve length flanked by evenly convex lateral areas ; ventral interarea slightly curved apsacline longer than anacline dorsal interarea, delthyrium and notothyrium open, pedicle callist usually conspicuous ; radial ornamentation costellate commonly 6 per mm, 2 mm antero-medially of the dorsal umbo ; branching simple, rarely developing secondaries especially externally (only 3 external costellae observed in sectors III and IV of 24 well-preserved exteriors).

Teeth small, supported by dental plates extending anteriorly for 23% the length of the pedicle valve and diverging for 130% their length ; ventral muscle field bilobed with diductor scars extending anteriorly for 35% the length of the pedicle valve but not surrounding the median adductor field ; *vascula media* slightly divergent, remaining mantle canal system obscure.

Cardinal process consisting of linear shaft and small rounded myophore ; brachiophores short divergent, with subparallel bases flanking well-developed notothyrial platform extending anteriorly for 22% of the length of the brachial valve and separated from each other by 97% of their length ; adductor scars poorly differentiated, suboval, situated on either side of low median ridge and extending anteriorly for 59% of the length of the brachial valve.

FIGURED MATERIAL.

	length	width (mm)
Internal mould of brachial valve (BB 35434)	4·0	–
Internal mould of pedicle valve (BB 35435)	3·5	–
Internal mould of brachial valve (BB 35436)	3·0	–
External mould of brachial valve (BB 35437)	4·0	–

HORIZON AND LOCALITY. Lower Llandeilo yellow-weathering calcareous sandstones exposed in quarry 300 yds west of Ysgubor-wen Farm, Llandeilo (Grid Ref. SN 644224).

Dalmanella salopiensis sp. nov.

(Pl. 15, figs. 5, 6, 8–12)

DIAGNOSIS. Small, ventribiconvex *Dalmanella* with a brachial valve 77% as long as wide and 15% as deep as long and fine costellae, rarely branching externally, commonly numbering 6 per mm at the 2 mm growth stage ; dental plates 21% as long as the pedicle valve and 159% as divergent as long ; ventral muscle scar extending anteriorly for 35% of the length of the pedicle valve ; subparallel brachiophore bases 22% as long as the brachial valve and separated from each other by 86% of their length.

DESCRIPTION. Small, subquadrate, ventribiconvex *Dalmanella* with obtuse cardinal angles ; pedicle valve 38% as deep as long with rounded carina medially and evenly sloping lateral areas, brachial valve 77% as long as wide and 15% as deep as long with shallow median sulcus about four-fifths as wide as valve length flanked by evenly convex lateral areas ; ventral interarea slightly curved apsacline, longer than anacline dorsal interarea, delthyrium and notothyrium open ; radial ornamentation of costellae commonly 6 per mm 2 mm antero-medially of the dorsal umbo ; branching simple, rarely developing externally with only 4 external ribs observed in 32 mature brachial valves.

Teeth supported by dental plates extending anteriorly for 21% the length of the pedicle valve and extending laterally to 159% of their length ; ventral muscle scar bilobed extending anteriorly for 35% of the length of the pedicle valve ; mantle canal system unknown.

Cardinal process consisting of linear shaft and compact myophore on a well-developed notothyrial platform ; brachiophores short, divergent with subparallel bases extending anteriorly for 22% of the length of the brachial valve and separated from each other by 86% of their length ; adductor scars suboval, faintly impressed on either side of low median ridge and extending anteriorly for 59% of the length of the brachial valve.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	External and internal moulds of brachial valve (BB 35446a, b)	3·0	3·8
PARATYPES	External and internal moulds of pedicle valve (BB 35447a, b)	3·2	3·7
	External and internal moulds of brachial valve (BB 35448a, b)	1·6	2·4
	External and internal moulds of brachial valve (BB 35449a, b)	1·7	2·5
	External and internal moulds of brachial valve (BB 35450a, b)	2·5	3·2

TYPE HORIZON AND LOCALITIES. Meadowtown Beds : BB 35446 from loose flags by the side of Minicop Farm (Grid Ref. SJ 314018) ; BB 35450 from flags in Quinton's Quarry in the field 200 yds north-east of the chapel at Meadowtown (Grid Ref. SJ 312013) ; BB 35448–9 from tuffaceous flags 100 yds south-east of Minicop Farm (Grid Ref. SJ 315018) ; BB 35447 from shales along Meadowtown–Rorrington road 220 yds from Meadowtown Chapel (Grid Ref. SJ 309012).

Dalmanella salopiensis gregaria sp. et subsp. nov.

(Pl. 15, figs. 13–16, 20)

DIAGNOSIS. Like *Dalmanella salopiensis* but with a brachial valve 74% as long as wide and 16% as deep as long ; dental plates 19% as long as the pedicle valve and 184% in lateral extent as long ; ventral muscle scar 36% as long as the pedicle valve ; subparallel brachiophore bases 23% as long as the brachial valve and separated from each other by 91% of their length.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	External and internal moulds of brachial valve (BB 35443a, b)	2·5	3·5
PARATYPES	External and internal moulds of pedicle valve (BB 35444a, b)	2·4	2·8
	External and internal moulds of brachial valve (BB 35445a, b)	–	2·8
	Internal and external moulds of pedicle valve (BB 35407a, b)	3·8	5·0

TYPE HORIZON AND LOCALITY. Spy Wood Grit exposed in north bank of Spy Wood Brook, 170 yds north-east of Spy Wood Cottage (Grid Ref. SO 282958).

Dalmanella salopiensis transversa sp. et subsp. nov.

(Pl. 15, figs. 17–19, 21–24; Pl. 16, fig. 1)

DIAGNOSIS. Like *Dalmanella salopiensis* but with a brachial valve 73% as long as wide and about one-tenth as deep as long; dental plates 20% as long as the pedicle valve and 192% in lateral extent as long; subparallel brachiophore bases 22% as long as the brachial valve.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	External and internal moulds of brachial valve (BB 35438a, b)	3·4	4·2
PARATYPES	External and internal moulds of pedicle valve (BB 35439a, b)	3·5	–
	External and internal moulds of brachial valve (BB 35440a, b)	2·5	3·5
	External and internal moulds of pedicle valve (BB 35441a, b)	2·5	3·0
	External and internal moulds of pedicle valve (BB 35442a, b)	2·5	3·2

TYPE HORIZON AND LOCALITY. Aldress Shales exposed in the bank of Ox Wood Dingle at the south-west corner of Ox Wood, just north of the Rorrington–Wotherton road (Grid Ref. SJ 290007).

DISCUSSION. *Dalmanella* is a common brachiopod in the Shelve successions. Apart from a *Dalmanella*-like species from the Mytton Flags which has been separately described, the genus is represented by a series of closely related stocks with small adult shells usually between 2 and 5 mm long ornamented by simply arranged costellae numbering 6 per mm 2 mm antero-medially of the dorsal umbo, and bearing a cardinal process with a small rounded myophore, well-developed subparallel brachiophore bases and the impressions of a bilobed ventral muscle field. These stocks occur in the Betton Beds to Aldress Shales inclusive but are very common in the Meadowtown Beds, the Spy Wood Grit and the Aldress Shales which have provided the data for the three samples listed in Tables 55 to 63.

At first sight, the stocks appear to be like the Lower Llandeilo *Dalmanella parva* Williams (1949 : 169) in the dimensions and proportions of their external and internal features. However, a sample of that species from the type locality proved to be significantly different from Shelve *Dalmanella* in a number of attributes. From all three samples *D. parva* differs in the rate of anterior expansion and in the inherently more acute divergence of its dental plates. The species further differs from the Meadowtown and Spy Wood forms in the relatively faster growth in width and, from the Aldress sample, in the inherently greater width of the brachial valve. The Llandeilo species also differs from the Meadowtown and Aldress stocks in the shape parameters and relative growth of the cardinalia.

In contrast to these decisive specific differences, the relationship between the three Shelve samples is much more complicated. The Meadowtown sample, herein recognized as the new species *D. salopiensis*, differs from both the Spy Wood and Aldress stocks in the more acutely divergent attitude of the dental plates; and additionally from the former in the residual length of the ventral muscle scar and the divergence of the brachiophore bases. It differs from the latter in the relative width of the brachial valve. Moreover there is also a significant difference $(p < 0{\cdot}001)$ in the residual shape of the brachial valve of the Aldress and Spy Wood samples. These relationships are most conveniently expressed by assuming that the Aldress and Spy Wood samples constitute two new subspecies, *D. salopiensis transversa* and *D. salopiensis gregaria* respectively.

The stratigraphic ranges of these taxa are well defined. The small number of moulds collected from the Betton Beds are indistinguishable from *D. salopiensis*. A larger sample of specimens from the Rorrington Beds, on the other hand, differs from *D. salopiensis* at least in the degree of divergence of the dental plates $(p < 0{\cdot}001)$, but they proved to be identical in every respect with the new Spy Wood subspecies *D. salopiensis gregaria*.

Neither *D. salopiensis* (s.l.) nor *D. parva* are like other Anglo-Welsh *Dalmanella*. *D. indica* (Whittington) appears to be most closely related, but comparisons of statistical data for that species (Williams 1963 : 382–385) with those for *D. parva* and *D. salopiensis* (s.l.) reveals significant differences in a number of features including the parallel disposition of the brachiophore bases in the older species and especially in the simplicity of their ribbing patterns which are essentially: $1\bar{a}$, 1, $2\bar{a}$, 2, $3\bar{a}$, $3\bar{b}$, 3, $4\bar{a}\bar{l}$, $4\bar{a}$, 4, $4a^{\circ}$.

TABLE 55

Statistics of length (l) and maximum width (w) of n brachial valves of *Dalmanella parva* Williams (A), *D. salopiensis* sp. nov. (B), *D. salopiensis gregaria* sp. et subsp. nov. (C) and *D. salopiensis transversa* sp. et subsp. nov. (D)

	A	B	C	D
n	42	82	46	14
$\bar{l}$ mm	2·76	2·06	2·28	2·62
(var l)	(0·54)	(0·461)	(0·443)	(0·814)
$\bar{w}$ mm	3·57	2·73	3·09	3·59
(var w)	(0·795)	(0·522)	(0·55)	(1·148)
r	0·986	0·972	0·955	0·993
$\overline{\log_e l}$	0·9808	0·6721	0·7845	0·9078
(var $\log_e l$)	(0·0685)	(0·1029)	(0·0815)	(0·1119)
$\overline{\log_e w}$	1·2429	0·9708	1·099	1·2364
(var $\log_e w$)	(0·0603)	(0·0675)	(0·0561)	(0·0851)
r_e	0·989	0·976	0·959	0·993
α	0·9384	0·81	0·8294	0·8723
(var α)	(0·00049)	(0·00038)	(0·00126)	(0·00088)

TABLE 56

Statistics of length (l) and thickness (th) of n pedicle valves of *Dalmanella parva* Williams (A), *D. salopiensis* sp. nov. (B), *D. salopiensis gregaria* sp. et subsp. nov. (C) and *D. salopiensis transversa* sp. et subsp. nov. (D)

	A	B	C	D
n	29	72	53	8
$\bar{l}$ mm	3·29	2·37	3·18	2·82
(var l)	(0·863)	(0·608)	(1·223)	(0·476)
$\overline{th}$ mm	1·04	0·91	1·35	1·01
(var th)	(0·092)	(0·089)	(0·0182)	(0·038)
r	0·909	0·881	0·933	0·885
a	0·3274	0·3827	0·3861	0·2839
(var a)	(0·00069)	(0·00046)	(0·00037)	(0·00291)

TABLE 57

Statistics of length (l) of n pedicle valves and length of dental plates (dl) of *Dalmanella parva* Williams (A), *D. salopiensis* sp. nov. (B), *D. salopiensis gregaria* sp. et subsp. nov. (C) and *D. salopiensis transversa* sp. et. subsp. nov. (D)

	A	B	C	D
n	52	102	69	11
$\bar{l}$ mm	3·35	2·22	2·92	2·69
(var l)	(0·654)	(0·609)	(1·159)	(0·685)
$\overline{dl}$ mm	0·78	0·46	0·57	0·53
(var dl)	(0·061)	(0·025)	(0·045)	(0·026)
r	0·882	0·88	0·907	0·919
$\overline{\log_e l}$	1·1807	0·7380	1·0063	0·9446
(var $\log_e l$)	(0·0564)	(0·1168)	(0·1279)	(0·0902)
$\overline{\log_e dl}$	−0·2978	−0·8268	−0·6292	−0·6749
(var $\log_e dl$)	(0·0957)	(0·1104)	(0·13)	(0·0868)
r_e	0·888	0·887	0·913	0·925
α	1·3026	0·9724	1·0082	0·9808
(var α)	(0·00717)	(0·00201)	(0·00253)	(0·01538)

TABLE 58

Statistics of length (l) and maximum anterior divergence (w) of the dental plates in n pedicle valves of *Dalmanella parva* Williams (A), *D. salopiensis* sp. nov. (B), *D. salopiensis gregaria* sp. et subsp. nov. (C) and *D. salopiensis transversa* sp. et subsp. nov. (D)

	A	B	C	D
n	53	77	56	8
$\bar{l}$ mm	0·79	0·46	0·55	0·53
(var l)	(0·07)	(0·024)	(0·046)	(0·021)
$\bar{w}$ mm	1·03	0·73	1·01	1·02
(var w)	(0·069)	(0·042)	(0·087)	(0·059)
r	0·951	0·805	0·879	0·901
$\overline{\log_e l}$	−0·2842	−0·8385	−0·6618	−0·6689
(var $\log_e l$)	(0·1054)	(0·1088)	(0·141)	(0·0729)
$\overline{\log_e w}$	−0·0055	−0·3462	−0·0282	−0·0028
(var $\log_e w$)	(0·0631)	(0·075)	(0·0812)	(0·0548)
r_e	0·955	0·813	0·886	0·907
α	0·774	0·8306	0·7588	0·8669
(var α)	(0·00103)	(0·00312)	(0·00229)	(0·02217)

TABLE 59

Statistics of length (l) of n pedicle valves and length of ventral muscle scar (sc) of *Dalmanella parva* Williams (A), *D. salopiensis* sp. nov. (B), *D. salopiensis gregaria* sp. et subsp. nov. (C) and *D. salopiensis transversa* sp. et subsp. nov. (D)

	A	B	C	D
n	44	69	61	8
$\bar{l}$ mm	3·33	2·44	3·06	2·74
(var l)	(0·608)	(0·474)	(1·099)	(0·608)
$\overline{sc}$ mm	1·17	0·83	1·12	0·87
(var sc)	(0·084)	(0·061)	(0·198)	(0·088)
r	0·914	0·853	0·899	0·969
$\overline{\log_e l}$	1·1775	0·8558	1·0619	0·968
(var $\log_e l$)	(0·0532)	(0·0763)	(0·1112)	(0·078)
$\overline{\log_e sc}$	0·1317	−0·2313	0·0388	−0·1877
(var $\log_e sc$)	(0·0592)	(0·0858)	(0·1468)	(0·1086)
r_e	0·92	0·861	0·905	0·9713
α	1·0554	1·06	1·1487	1·1804
(var α)	(0·00408)	(0·00434)	(0·00403)	(0·01315)

TABLE 60

Statistics of length (l) of n brachial valves and length of brachiophore bases (lc) of *Dalmanella parva* Williams (A), *D. salopiensis* sp. nov. (B), *D. salopiensis gregaria* sp. et subsp. nov. (C) and *D. salopiensis transversa* sp. et subsp. nov. (D)

	A	B	C	D
n	38	121	55	22
$\bar{l}$ mm	3·11	2·18	2·56	2·48
(var l)	(0·473)	(0·517)	(0·474)	(0·811)
$\overline{lc}$ mm	0·69	0·49	0·58	0·55
(var lc)	(0·027)	(0·025)	(0·023)	(0·027)
r	0·814	0·911	0·884	0·917
$\overline{\log_e l}$	1·1118	0·726	0·906	0·8472
(var $\log_e l$)	(0·0476)	(0·1036)	(0·0695)	(0·1236)
$\overline{\log_e lc}$	−0·3913	−0·7675	−0·5684	−0·6404
(var $\log_e lc$)	(0·0543)	(0·1005)	(0·0661)	(0·0851)
r_e	0·822	0·915	0·889	0·922
α	1·068	0·985	0·9751	0·8299
(var α)	(0·01028)	(0·00132)	(0·00376)	(0·00513)

TABLE 61

Statistics of length (l) and maximum lateral extension (w) of the brachiophore bases in n brachial valves of *Dalmanella parva* Williams (A), *D. salopiensis* sp. nov. (B), *D. salopiensis gregaria* sp. et subsp. nov. (C) and *D. salopiensis transversa* sp. et subsp. nov. (D)

	A	B	C	D
n	46	118	52	21
$\bar{l}$ mm	0·65	0·49	0·58	0·57
(var l)	(0·025)	(0·025)	(0·023)	(0·022)
$\bar{w}$ mm	0·63	0·42	0·53	0·48
(var w)	(0·021)	(0·008)	(0·013)	(0·013)
r	0·778	0·771	0·596	0·741
$\overline{\log_e l}$	−0·4617	−0·765	−0·5718	−0·6008
(var $\log_e l$)	(0·0587)	(0·0993)	(0·0667)	(0·0656)
$\overline{\log_e w}$	−0·4811	−0·8848	−0·665	−0·7653
(var $\log_e w$)	(0·0496)	(0·0422)	(0·0452)	(0·0567)
r_e	0·787	0·781	0·604	0·75
α	0·9188	0·652	0·8228	0·9303
(var α)	(0·0073)	(0·00142)	(0·00859)	(0·01993)

TABLE 62

Statistics of length (l) of n brachial valves and length of adductor scars from umbo (sc) of *Dalmanella parva* Williams (A), *D. salopiensis* sp. nov. (B) and *D. salopiensis gregaria* sp. et subsp. nov. (C)

	A	B	C
n	13	24	22
$\bar{l}$ mm (var l)	3·45 (0·411)	2·74 (0·505)	2·74 (0·5)
$\overline{sc}$ mm (var sc)	1·99 (0·207)	1·56 (0·149)	1·6 (0·152)
r	0·906	0·925	0·929
a (var a)	0·7104 (0·00821)	0·5439 (0·00194)	0·5518 (0·00207)

TABLE 63

The distribution of brachial valves of *Dalmanella parva* Williams (A), *D. salopiensis* sp. nov. (B), *D. salopiensis gregaria* sp. et subsp. nov. (C) and *D. salopiensis transversa* sp. et subsp. nov. (D) with 4–8 costellae per mm, 2 mm antero-medially of the dorsal umbones

	Costellae per mm				
	4	5	6	7	8
A	1	4	8	6	3
B	1	11	17	3	–
C	2	5	9	–	–
D	–	2	2	2	–

Dalmanella elementaria sp. nov.

(Pl. 16, figs. 2–8)

DIAGNOSIS. Very small, ventribiconvex, sulcate *Dalmanella* with a finely costellate ornamentation, faintly impressed bilobed ventral muscle field, slightly divergent dental plates, a short ridge-like cardinal process, subtriangular blade-like brachiophores with subparallel bases and small fulcral plates.

DESCRIPTION. Very small, ventribiconvex, subquadrate *Dalmanella* with rounded, obtuse cardinal angles ; pedicle valve slightly carinate medially, one-third as deep as long ; gently convex brachial valve very rarely more than 3 mm long with a mean length relative to width of 78·3% (variance 109·2) for 5 valves, median sulcus usually persistent, rounded, almost three-fifths as wide as the valve length, bounded by evenly convex lateral areas ; ventral and dorsal interareas short, apsacline and anacline respectively, with an open delthyrium containing a small pedicle callist and an open notothyrium ; ribbing very fine with 7 and 8 costellae per mm, 2 mm antero-medially of the umbones of 5 and 2 brachial valves respectively, first three sectors narrow with simple branching normally consisting of 1ā, 1, 2ā, 2b̄, 2, 3āl̄, 3ā, 3, 3a°.

Teeth supported by slightly divergent dental plates extending forward for an average of 26·3% (variance 46·8) the length of 5 valves ; ventral muscle field rarely and faintly impressed, apparently bilobed, with shorter median adductor scar flanked by lobate diductors.

Cardinal process consisting of a low impersistent ridge not extending to posterior margin of notothyrium, brachiophores subtriangular, blade-like with subparallel bases extending anteriorly for one-fifth the length of the valve (mean lengths and variances of 13 valves and brachiophore bases = 1·99 (0·256) and 0·41 (0·019) respectively ; r = 0·943) ; sockets narrow, defined by small fulcral plates.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	External and internal moulds of brachial valve (BB 35352a, b)	3·2	3·8

		length	width (mm)
PARATYPES	External and internal moulds of pedicle valve (BB 35353a, b)	2·5	3·5
	External and internal moulds of pedicle valve (BB 35354a, b)	1·8	–
	External and internal moulds of brachial valve (BB 35355a, b)	3·0	–
	External and internal moulds of brachial valve (BB 35356a, b)	2·0	3·0
	External and internal moulds of brachial valve (BB 35357a, b)	2·5	–

TYPE HORIZON AND LOCALITIES. Mytton Flags (Shelve Church Member): BB 35353a, b from exposures in road level north of Wood House (Grid Ref. SJ 338003), all other specimens from a trench cut 1 ft above road level near Shelve Church (Grid Ref. SO 335990).

DISCUSSION. Among the fossils recovered from the Mytton Flags, there quite commonly occur impressions of a small costellate, thin-shelled orthide which have all the essential characters expected of early enteletaceans. The combination of such features is so striking that, although there is, as yet, no proof, such as the presence of microscopic moulds of puncta, of their enteletacean affinities, they have been identified as primitive *Dalmanella*. Certainly they are strongly reminiscent of young *Dalmanella* in many respects, yet there are characters that immediately distinguish these Arenig forms from all other described *Dalmanella*. Among these are the fineness and simple arrangement of costellae and the ridge-like cardinal process which did not extend the length of the notothyrial platform nor become differentiated into myophore and shaft as in other species assigned to the genus. Not only do these features render the new species unique among known *Dalmanella* but, together with the obscurity of muscle impressions and simplicity of brachiophore arrangement, are also the features one would expect to find in a stock that was ancestral to the more typical Ordovician *Dalmanella*. Indeed when more is known about these Arenigian stocks, they may prove to be so distinctive in the generalized nature of their cardinalia as to constitute a distinct species group within the *Dalmanella* taxon.

ONNIELLA Bancroft 1928

Onniella ostentata Williams ***lepida*** subsp. nov.

(Pl. 16, figs. 9–14)

DIAGNOSIS. Like *Onniella ostentata* Williams (1963 : 405) but with finer costellae numbering 4 to 6 per mm at the 5 mm growth stage, shorter dental plates which grew forward more slowly and a massive bilobed cardinal process not united to the brachiophores in adult shells.

DESCRIPTION. Small, ventribiconvex *Onniella* with obtusely rounded cardinal angles; pedicle valve 23% as deep as long with a subcarinate rounded median zone and evenly sloping to slightly concave lateral areas, brachial valve 76% as wide and 11% as deep as long with a shallow narrow to weak sulcus; ventral interarea planar apsacline, longer than anacline dorsal interarea, delthyrium and notothyrium open, pedicle callist usually well developed; radial ornamentation of costellae commonly 4 per mm, 5 mm antero-medially of dorsal umbo, external costellae poorly developed in sectors III and IV.

Teeth small trigonal, supported by dental plates extending anteriorly for 16% of the length of the pedicle valve and diverging for 49% of their length; ventral muscle field bilobed with the diductor scars extending anteriorly for 29% of the length of the pedicle valve and flanking a shorter submedial adductor scar; *vascula media* proximally divergent, remaining mantle canal system unknown.

Cardinal process consisting of linear shaft and rounded myophore in early growth stages but usually massive and medially cleft in valves more than 3 mm long; brachiophores short, acutely divergent, with bases, which may be broad and indented by a pit, extending forward for 19% of the length of the brachial valve and splaying laterally for 58% of their length; sockets well defined but without fulcral plates; adductor scars suboval, impressed on either side of median ridge and extending anteriorly for 57% of the length of the valve; mantle canal system unknown.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	External and internal moulds of brachial valve (BB 35456a, b)	4·3	5·0
PARATYPES	External and internal moulds of pedicle valve (BB 35455a, b)	4·8	6·0
	External and internal moulds of brachial valve (BB 35457a, b)	3·0	4·0
	Internal mould of brachial valve (BB 35458)	4·0	–

TYPE HORIZON AND LOCALITY. Aldress Shales exposed in the bank of Ox Wood Dingle at the south-west corner of Ox Wood, just north of the Rorrington–Wotherton road (Grid Ref. SJ 290007).

DISCUSSION. Except for the complementary moulds of a brachial valve (BB 35572a, b) collected from the Spy Wood Grit (Pl. 16, figs. 15, 18), *Onniella* is restricted in the Shelve area to the Aldress and Whittery Shales. Although it is not very common in either formation, two small samples were available for study. They proved to be alike in every respect (Tables 64–72) and obviously represent the same species. They are however significantly different from penecontemporaneous *Onniella*, such as *O. soudleyensis* (Bancroft 1945 : 210) and *O. ostentata* (Williams 1963 : 405). In comparison with the former species, the Shelve *Onniella* differs in the more elongate growth of the brachial valve, the relative length and narrowness of the cardinalia and in the early development of a massive bilobed cardinal process. In respect of the last-named feature the Shelve *Onniella* is nearer *O. ostentata* s.s. except that the cardinal process always remains discrete from the brachiophores. In other features, too, there is a noteworthy likeness between the two stocks which differ only in the relative shortness of the dental plates and the fineness of ribbing and poor development of secondary externals in sectors III and IV in the Shelve samples. In the Whittery sample, 4, 5 and 6 costellae per mm were counted 5 mm antero-medially of the umbones of 3, 1 and 1 brachial valves ; while $3\bar{a}\bar{l}\bar{a})3a^\circ$, $3\bar{c})3a^\circ$ and $4\bar{b})4b^\circ$ occurred in 0/4, 1/5 and 1/2 brachial valves respectively. These differences seem to be important enough to merit subspecific recognition.

TABLE 64

Statistics of length (l) and maximum width (w) of n brachial valves of *Onniella ostentata lepida* subsp. nov. from the Aldress Shales (A) and Whittery Shales (B)

	A	B
n	11	22
$\bar{l}$ mm (var l)	3·2 (0·638)	3·7 (1·149)
$\bar{w}$ mm (var w)	4·12 (0·748)	4·99 (2·006)
r	0·985	0·962
$\overline{\log_e l}$ (var $\log_e l$)	1·1331 (0·0604)	1·2694 (0·0804)
$\overline{\log_e w}$ (var $\log_e w$)	1·394 (0·0429)	1·5679 (0·0775)
r_e	0·99	0·965
α (var α)	0·843 (0·00158)	0·9815 (0·00329)

TABLE 65

Statistics of length (l) and depth (th) of 12 brachial valves of *Onniella ostentata lepida* subsp. nov. from the Whittery Shales

$\bar{l}$ mm (var l)	4·22 (0·532)
$\overline{th}$ mm (var th)	0·48 (0·012)
r	0·865
a (var a)	0·1527 (0·00058)

TABLE 66

Statistics of length (l) and depth (th) of 10 pedicle valves of *Onniella ostentata lepida* subsp. nov. from the Whittery Shales

$\bar{l}$ mm (var l)	3·91 (0·761)
$\overline{th}$ mm (var th)	0·88 (0·068)
r	0·493
a (var a)	0·3 (0·00851)

TABLE 67

Statistics of length (l) of n pedicle valves and length of dental plates (dl) of *Onniella ostentata lepida* subsp. nov. from the Aldress Shales (A) and Whittery Shales (B)

	A	B
n	9	12
$\bar{l}$ mm (var l)	3·42 (1·017)	3·91 (1·788)
$\overline{dl}$ mm (var dl)	0·57 (0·034)	0·6 (0·061)
r	0·799	0·909
a (var a)	0·184 (0·00175)	0·185 (0·00059)

TABLE 68

Statistics of length (l) and maximum anterior divergence (w) of the dental plates in n pedicle valves of *Onniella ostentata lepida* subsp. nov. from the Aldress Shales (A) and Whittery Shales (B)

	A	B
n	9	9
$\bar{l}$ mm (var l)	0·57 (0·034)	0·52 (0·026)
$\bar{w}$ mm (var w)	1·21 (0·081)	1·01 (0·079)
r	0·858	0·877
a (var a)	1·5346 (0·0885)	1·7305 (0·09891)

TABLE 69

Statistics of length (l) of n pedicle valves and length of ventral muscle scar of *Onniella ostentata lepida* subsp. nov. from the Aldress Shales (A) and Whittery Shales (B)

	A	B
n	9	10
$\bar{l}$ mm mm (var l)	3·42 (1·017)	3·99 (1·774)
$\overline{sc}$ mm (var sc)	1·04 (0·109)	1·11 (0·225)
r	0·915	0·882
a (var a)	0·3268 (0·00248)	0·3564 (0·00352)

TABLE 70

Statistics of length (l) of n brachial valves and length of brachiophore bases (lc) of *Onniella ostentata lepida* subsp. nov. from the Aldress Shales (A) and Whittery Shales (B)

	A	B
n	16	21
$\bar{l}$ mm (var l)	3·19 (0·652)	4·13 (0·981)
$\overline{lc}$ mm (var lc)	0·66 (0·021)	0·69 (0·027)
r	0·681	0·913
a (var a)	0·1812 (0·00125)	0·1655 (0·00023)

TABLE 71

Statistics of length (l) and maximum lateral extension (w) of the brachiophore bases in n brachial valves of *Onniella ostentata lepida* subsp. nov. from the Aldress Shales (A) and Whittery Shales (B)

	A	B
n	16	15
$\bar{l}$ mm (var l)	0·66 (0·021)	0·66 (0·025)
$\bar{w}$ mm (var w)	1·1 (0·075)	1·19 (0·146)
r	0·803	0·967
$\overline{\log_e l}$ (var $\log_e l$)	−0·4405 (0·048)	−0·4437 (0·0566)
$\overline{\log_e w}$ (var $\log_e w$)	0·0654 (0·0597)	0·1279 (0·0977)
r_e	0·811	0·972
α (var α)	1·1157 (0·03045)	1·3139 (0·00719)

TABLE 72

Statistics of length (l) of n brachial valves and length of adductor scars (sc) of *Onniella ostentata lepida* subsp. nov. from the Aldress Shales (A) and Whittery Shales (B)

	A	B
n	15	10
$\bar{l}$ mm (var l)	3·2 (0·696)	4·27 (1·438)
$\overline{sc}$ mm (var sc)	1·88 (0·235)	2·3 (0·4)
r	0·833	0·979
a (var a)	0·581 (0·00794)	0·5274 (0·00146)

Family **HARKNESSELLIDAE** Bancroft 1928

HARKNESSELLA Reed 1917

Harknessella cf. ***subplicata*** Bancroft

(Pl. 16, fig. 16)

An incomplete internal mould (BB 35427), about 3 mm long, from the Spy Wood Grit exposed on top of the ridge 1440 yds NNE of Rorrington bench mark 599 (Grid Ref. SJ 303018), appears to represent the immature brachial valve of a *Harknessella*. The semi-oval valve was about three-fifths as long as wide and almost one-fifth as deep as long with a well-developed median sulcus over half as wide as the valve length and gently convex lateral areas. Ribbing impressions on the mould reach almost to the cardinalia and suggest a coarsely costellate arrangement with about 4 per mm towards the anterior margin. The cardinalia consisted of a cardinal process differentiated into a stout shaft and crenulated myophore, obliquely disposed sockets defined by fulcral plates and brachiophores supported by acutely divergent bases indented submedially by deep adductor pits.

The development of adductor pits and the disposition of the brachiophore bases and fulcral plates to give the 'angulated subparallel pre-socket lines' of Bancroft (1945 : 225) indicate that the brachial valve belonged to *Harknessella* ; the relative coarseness of the ribbing further suggests its close affinities with the species *H. subplicata* Bancroft (1945 : 226) from the Coston Sandstone of E. Shropshire.

HORDERLEYELLA Bancroft 1928

Horderleyella cf. ***plicata*** Bancroft

(Pl. 16, figs. 17, 19, 20 ; Pl. 17, fig. 1)

DIAGNOSIS. Small, subquadrate *Horderleyella* ornamented by 3 to 5 fascicostellae per mm, 2 mm antero-medially of the dorsal umbo ; bilobed ventral muscle scar extending anteriorly for about two-fifths the valve length ; cardinal process blade-like, subparallel brachiophores extending forward for about 12% of the valve length and dorsal adductor scars impressed posteriorly in shallow hollows in the notothyrial platform.

DESCRIPTION. Small, subquadrate, ventribiconvex *Horderleyella* with cardinal angles approximating to 90° ; pedicle valve carinate medially, 30% as deep as long ;

brachial valve 76% as long as wide and 12% as deep as long with a strong median sulcus about two-thirds as wide as the valve length, flanked by flattened lateral areas; ventral and dorsal interareas planar, apsacline and anacline respectively with open delthyrium and notothyrium; radial ornamentation fascicostellate with subangular ribs branching internally and numbering 3, 4 and 5 per mm, 2 mm anteromedially of the umbones of 1, 2 and 1 brachial valves.

Teeth supported by divergent dental plates extending forward for 22% of the length of the valve; ventral muscle scar bilobed, about as wide as long, with subtriangular diductor impressions extending forward for 40% the length of the valve but not enclosing the shorter median adductor scar.

Cardinal process simple, blade-like, brachiophores narrowly divergent with subparallel bases extending forward for 18% of the length of the brachial valve and deeply separated from well-developed fulcral plates defining splayed sockets; adductor scars lightly impressed on either side of the wide median ridge except posteriorly where they are inserted as a pair of shallow hollows into the notothyrial platform.

FIGURED MATERIAL.

	length	width (mm)
External and internal moulds of pedicle valve (BB 35431a, b)	6·0	6·5
Internal mould of brachial valve (BB 35432)	3·5	4·0
Internal mould of brachial valve (BB 35433)	4·0	–

HORIZONS AND LOCALITIES. Spy Wood Grit: BB 35431 from exposures on top of ridge 1440 yds NNE of Rorrington bench mark 599 (Grid Ref. SJ 303018): BB 35432 from exposures 1100 yds north-east of Rorrington (Grid Ref. SJ 303015). Aldress Shales: BB 35433 from exposures in bank of Ox Wood Dingle at south-west corner of Ox Wood a few yards north of the Rorrington–Wotherton road (Grid Ref. SJ 290007).

DISCUSSION. A small number of moulds of *Horderleyella*, mainly those of brachial valves, have been recovered from the Spy Wood Grit and Aldress Shales. They appear to be conspecific with *H. plicata* Bancroft (1928: 186; 1945: 236) from the Costonian and Harnagian successions of E. Shropshire, especially in the radial ornamentation and the shape and internal morphology of the brachial valve. The differentiation of the cardinal process of *H. plicata* into myophore and shaft is probably not a diagnostic feature in view of the much smaller size of the Shelve specimens. Such differences in shell size may also account for the relative delicacy of the cardinalia of *H. subcarinata* MacGregor (1961: 193) from the Upper Llandeilo of the Berwyn Hills which may also be conspecific with *H. plicata*.

In contrast to the close similarity of the brachial valves, the Shelve pedicle valves may prove to be relatively deeper and the ventral muscle scar wider and shorter, being only 79% as wide as long and 31% of the length of three pedicle valves of *H. plicata*. Larger collections, however, might indicate that these differences fall within the range of variability of *H. plicata* and, provisionally at least, the Shelve material can be identified as that species.

Horderleyella sp.

(Pl. 17, figs. 2, 3)

The external and internal moulds of an immature pedicle valve of *Horderleyella*, 2·8 mm long and 3·5 mm wide (BB 35420a, b), have been recovered from the Meadowtown Beds exposed in the lane side 370 yds north-west of Meadowtown Chapel (Grid Ref. SJ 311015).

The valve was subquadrate in outline with obtuse cardinal angles and about one-quarter as deep as long in the vicinity of a strong narrow median carina although the lateral areas are only very gently convex. The radial ornamentation was strongly fascicostellate with a count of 4 ribs per mm, 2 mm anterior of the umbo. Internally, divergent dental plates, extending anteriorly for almost one-fifth the length of the valve, formed the posterior boundaries of a subpentagonal ventral muscle scar which was about three-quarters as long as wide and extended forward for about three-tenths the valve length.

The valve cannot be placed unequivocally in any of the described species of *Horderleyella*. The relatively fine fascicostellate ornamentation is more diagnostic of the Upper Llanvirn *Horderleyella convexa* Williams (1949 : 171), for which counts of 3, 4 and 5 costellae per mm have been obtained 2 mm anterior of the umbones of 1, 2 and 2 brachial valves respectively. The muscle scar, however, is very much wider than even that of *H. convexa* ; and, although this difference is likely to be attributable to the immaturity of the shell, more material will have to be obtained before specific identification is merited.

REUSCHELLA Bancroft 1928

Reuschella horderleyensis Bancroft ***carinata*** subsp. nov.

(Pl. 17, figs. 4–9)

DIAGNOSIS. Subquadrate *Reuschella* with a narrowly carinate and laterally flattened pedicle valve about 23% as deep as long and a deeply sulcate brachial valve 73% as long as wide and 15% as deep as long ; radial ornamentation coarsely fascicostellate with 2 or 3 ribs per mm, 10 mm anteriorly of the dorsal umbo and poorly developed external branching except in the lateral sectors ; ventral muscle scar slightly bilobed and about one-third as long as the pedicle valve ; brachiophore bases extending forward for 14% of the length of the brachial valve.

DESCRIPTION. Ventribiconvex, subquadrate *Reuschella* with acute cardinal angles in specimens up to 14 mm long but usually becoming obtuse in mature shells, brachial valve 73% as long as wide and 15% as deep as long with a narrowly rounded sulcus having a mean width relative to the length of 4 valves of 47% (range 39% to 55%) ; pedicle valve with a mean depth relative to length of 23% for 3 specimens representing the elevation of a narrow rounded carina flanked by flattened, rarely undulate lateral areas ; ventral and dorsal interareas well developed, apsacline and anacline respectively with open delthyrium and notothyrium ; radial ornamentation coarsely fascicostellate with counts of 2 and 3 ribs per mm, 10 mm anteriorly of the umbones of 4 and 3 brachial valves, external branching poorly developed but progressively earlier in lateral sectors.

Teeth strong with well-developed crural fossettes supported by divergent dental plates with an average forward extension relative to the length of 6 pedicle valves of 19% (range 17% to 22%); ventral muscle scar bilobed, 83% as wide as long in 12 pedicle valves (range 72% to 104%), extending anteriorly for 34% of the length of 7 valves (range 28% to 39%) and consisting of a broad median adductor impression not enclosed by subtriangular diductor tracks; mantle canal system probably lemniscate.

Cardinal process consisting of a massive shaft with serrated ridge-like myophore embedded in a thickened notothyrial platform indented anteriorly by shallow pits for the insertion of adductor muscle bases; brachiophores divergent, blade-like defining crenulated sockets; muscle impressions unknown.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	External and internal moulds of pedicle valve (BB 35513a, b)	13·5	17·0
PARATYPES	External and internal moulds of brachial valve (BB 35514a, b)	13·5	19·0
	Incomplete external mould of pedicle valve (BB 35515)	13·5	–
	Incomplete internal mould of brachial valve (BB 35516)	13·0	–
	Incomplete external and internal moulds of pedicle valve (BB 35517a, b)	13·5	–
	Incomplete external and internal moulds of brachial valve (BB 35518a, b)	12·5	–
	Incomplete external and internal moulds of brachial valve (BB 35519a, b)	4·0	–

HORIZON AND LOCALITIES. Whittery Shales: BB 35516 and BB 35519 from exposures about half-way down path going south to valley bottom below Marrington Farm (Grid Ref. SO 272967); the remainder from lower part of western bank of River Camlad 60 yds north-east of Marrington Farm (Grid Ref. SO 272970).

DISCUSSION. The *Reuschella* occurring in the Whittery and Hagley Shales are related to the early Caradocian *R. horderleyensis* (s.l.) which is widespread in E. Shropshire and Wales (Bancroft 1945: 239; Williams 1963: 413). However, comparisons with *R.* cf. *horderleyensis* and *R. horderleyensis undulata* from the Bala area (Williams 1963: 415–417) show differences exist which merit taxonomic recognition. In the outline of the shell and of the ventral muscle scar and its forward extension as well as the texture and branching of their radial ornamentation, the Shelve specimens are indistinguishable from *R. horderleyensis* and the Welsh subspecies. They do, however, differ from both taxa in being much flatter laterally and additionally from *R. horderleyensis* in the growth of the cardinalia. It seems appropriate, therefore, to recognize the Shelve sample as a new subspecies of *R. horderleyensis*.

TABLE 73

Statistics of length (l) and maximum width (w) of 7 brachial valves of *Reuschella horderleyensis carinata* subsp. nov.

$\bar{l}$ mm (var l)	10·00 (28·5)
$\bar{w}$ mm (var w)	13·73 (41·199)
r	0·993
$\overline{\log_e l}$ (var $\log_e l$)	2·1772 (0·2506)
$\overline{\log_e w}$ (var $\log_e w$)	2·5206 (0·1976)
r_e	0·995
α (var α)	0·8879 (0·00155)

TABLE 74

Statistics of length (l) and thickness (th) of 7 brachial valves of *Reuschella horderleyensis carinata* subsp. nov.

$\bar{l}$ mm (var l)	11·31 (20·841)
$\overline{th}$ mm (var th)	1·74 (0·556)
r	0·811
a (var a)	0·1633 (0·00182)

TABLE 75

Statistics of length (l) and length of brachiophore bases (lc) in 9 brachial valves of *Reuschella horderleyensis carinata* subsp. nov.

$\bar{l}$ mm (var l)	12·69 (16·259)
$\overline{lc}$ mm (var lc)	1·81 (0·196)
r	0·883
a (var a)	0·1098 (0·00037)

TABLE 76

Statistics of length (l) and maximum lateral extension (w) of the brachiophore bases of 8 brachial valves of *Reuschella horderleyensis carinata* subsp. nov.

$\bar{l}$ mm (var l)	1·96 (0·103)
$\bar{w}$ mm (var w)	3·99 (0·373)
r	0·771
a (var a)	1·9052 (0·24495)

Family **HETERORTHIDAE** Schuchert & Cooper 1931

HETERORTHIS Hall & Clarke 1892

Heterorthis sp.

(Pl. 17, figs. 10–14)

DIAGNOSIS. Small, semi-elliptical, plano- to concavo-convex *Heterorthis* with parallel-sided, bilobed ventral muscle scar 42% as long as the pedicle valve and a simple, median, plate-like cardinal process.

DESCRIPTION. Small, semi-elliptical, plano- to concavo-convex *Heterorthis* with cardinal angles approximating to 90°; pedicle valve about one-tenth as deep as long, slightly carinate medially; brachial valve averaging 80% as long as wide for 5 valves, plane to gently concave with a slight median sulcus; ventral and dorsal interareas planar, apsacline and anacline respectively, delthyrium open, notothyrium covered by chilidium; radial ornamentation costellate with low rounded ribs numbering 5 per mm, 2 mm antero-medially of umbo.

Teeth small, supported by divergent dental plates; ventral muscle field parallel-sided and elongately bilobed extending forward for an average of 42% the length of 3 pedicle valves and only slightly narrower than long.

Cardinal process consisting of a simple median plate with slightly splayed posterior surface, embedded in well-developed notothyrial platform, brachiophores plate-like acutely divergent, sockets simple without bounding fulcral plates; adductor scars elongately oval impressed on either side of low median ridge, extending anteriorly for over half the valve length.

FIGURED MATERIAL.

	length	width (mm)
External and internal moulds of pedicle valve (BB 35423a, b)	4·0	–
External and internal moulds of brachial valve (BB 35424a, b)	4·5	5·5

HORIZON AND LOCALITY. Spy Wood Grit exposed 1100 yds NNE of Rorrington (Grid Ref. SJ 303015).

DISCUSSION. The *Heterorthis* collected from the Shelve area consist of only 12 valves from the Spy Wood Grit and one from the Aldress Shales. The largest of these specimens was not more than 5 mm long and, although one would expect some mature shells even in the small sample available, there is a strong possibility that the collections are moulds of young shells. Indeed the undifferentiated cardinal process and the relatively modest development of the notothyrial platform suggest that this is so; and until more is known about the age structure of such samples, infrageneric recognition is withheld. In that respect the only clue to specific affiliation is given by the relatively poor development of the lateral diductor lobes in the manner of adult *H. retrorsistria* M'Coy (Williams 1963 : 420) although even that character may be merely diagnostic of immaturity.

TISSINTIA Havlíček 1970

1970 *Tissintia* Havlíček : 14.

When Havlíček proposed *Tissintia* as a new genus, he rightly emphasized its close relationship with *Heterorthis*. In consideration of the stratigraphic distribution of the only species recognized by him as belonging to the genus, he concluded that the stock bore many attributes of the prototypic heterorthid (Havlíček 1970 : 9–10). The planoconvex to ventribiconvex profile, the bilobed cardinal process and the disposition of the brachiophores in the even older *T. prototypa* confirm his identification of the changes such features underwent to give rise to the characteristics of the

Caradocian heterorthids. The reflexed costellae along the posterior edges of the shells of all heterorthids are especially interesting because well-preserved specimens from the Weston Beds show corresponding follicular embayments indenting the hinge-lines of both valves. These embayments indicate the presence, at some time or another, of backward-projecting setae. Whether functional setae persisted much within the cardinal angles is doubtful because the embayments may have been incorporated within laterally expanding hinge-lines after they had ceased to accommodate setae.

With regard to the origin of the heterorthids, the existence of so typical a *Tissintia* species as *prototypa* in the Lower Llanvirn suggests that *Paurorthis*, the earliest forms of which are not much older, may not be ancestral to the Heterorthidae as Havlíček (1970 : 16) believed. Indeed as in many other brachiopod groups, proposed lines of descent can be no more than tentative guesses until more is known of the Tremadoc–Arenig faunas.

Tissintia prototypa (Williams) emended A. W.

(Pl. 17, figs. 15–19 ; Pl. 18, figs. 1–9, 11)

1949 *Dalmanella prototypa* Williams : 168.

Diagnosis. Subcircular, ventribiconvex *Tissintia* with fine costellae reflexed posteriorly along the hinge-line and numbering 5 per mm, 5 mm antero-medially of the dorsal umbo ; brachiophore plates parallel with median ridge with bases extending anteriorly for 15% of the length of the brachial valve and 110% of their lateral spread ; ventral muscle field elongately bilobed, extending forward for 38% of the length of the pedicle valve.

Description. Subcircular, ventribiconvex to rarely planoconvex *Tissintia* with obtuse cardinal angles ; pedicle valve 21% as deep as long with an evenly convex median zone and flattened lateral areas, brachial valve 80% as long as wide and about one-tenth as deep as long or rarely planar, shallow median sulcus dying out on average 5 mm anterior of dorsal umbo (variance 0·016 for 10 valves), lateral areas flattened or slightly concave ; ventral interarea planar, apsacline, longer than anacline dorsal interarea, delthyrium and notothyrium open ; radial ornamentation fascicostellate commonly 5 per mm, 5 mm antero-medially of the dorsal umbo, external branches poorly developed in the first four sectors, costellae reflexed posterolaterally so that corresponding follicular embayments indent the internal surfaces of the hinge-lines of both valves.

Teeth small, trigonal, supported by dental plates extending anteriorly for 14% of the length of the pedicle valve and diverging for twice their length ; ventral muscle field elongately bilobed divided by a pair of fine median ridges extending forward from conspicuous pedicle callist ; adductor scars small, elongately oval, submedially situated ; diductor scars impressed anteriorly for 38% of the length of the pedicle valve but not enclosing adductors, adjustor scars impressed on the median surfaces of the dental plates ; mantle canal pattern lemniscate.

Cardinal process with bilobed myophore and long shaft on well-developed notothyrial platform passing anteriorly into median ridge ; brachiophores triangular in outline, acutely divergent, brachiophore bases parallel, ankylosed to median ridge and extending anteriorly for 15% of the length of the brachial valve, sockets oblique, bounded ventrally by brachiophores but not defined laterally by fulcral plates ; quadripartite adductor scars 46% as long as the valve ; adjustor scars small oval, located on median ridge anterior to notothyrial platform, mantle canal pattern lemniscate.

FIGURED MATERIAL.

	length	width (mm)
Internal mould of brachial valve (BB 35305)	6·0	7·0
Internal mould of pedicle valve (BB 35306)	9·0	10·0
External mould of brachial valve (BB 35307)	7·5	9·0
External mould of brachial valve (BB 35308)	8·0	9·5
Internal mould of brachial valve (BB 35309)	14·0	16·0
Incomplete internal mould of brachial valve (BB 35310)	–	–
External and internal moulds of pedicle valve (BB 35311a, b)	14·0	20·5
External and internal moulds of pedicle valve (BB 35312a, b)	12·5	15·0
External and internal moulds of brachial valve (BB 35313a, b)	13·0	20·0
External and internal moulds of brachial valve (BB 35314a, b)	13·0	16·0
External and internal moulds of brachial valve (BB 35315a, b)	12·0	14·0

HORIZONS AND LOCALITIES. BB 35305–35310 from Lower Llanvirn ashy shales exposed in stream 240 yds west of Llwyn Bedw Farm, Llandeilo (Grid Ref. SN 653212) ; BB 35311, BB 35314, BB 35315 from Weston Beds exposed 210 yds south-east of road crossing Betton Dingle, Lyde (Grid Ref. SJ 317015) ; BB 35313 from Weston Beds at Cwm Dingle 640 yds south of Little Weston (Grid Ref. SO 294978) ; BB 35312 from Weston Beds in road exposure 430 yds south-west of Miner's Arms, Priestweston (Grid Ref. SO 291970).

Tissintia immatura (Williams) emended A. W.

(Pl. 18, figs. 10, 12–15 ; Pl. 19, figs. 1–5)

1949 *Resserella immatura* Williams : 165.

DIAGNOSIS. Subcircular, planoconvex *Tissintia* with subcarinate pedicle valve 31% as deep as long, costellae reflexed posteriorly along the hinge-line and commonly numbering 3 per mm 5 mm antero-medially of the dorsal umbo ; brachiophore bases normally thickened to extend anteriorly for 17% of the length of the brachial valve and 84% of their lateral spread ; ventral muscle field elongately bilobed extending forward for 38% of the length of the pedicle valve.

DESCRIPTION. Subcircular, planoconvex to more rarely ventribiconvex with obtuse cardinal angles ; pedicle valve 31% as deep as long with a slightly carinate median zone and gently convex lateral areas ; brachial valve 79% as long as wide, gently convex or more commonly planar with indistinct sulcus ; ventral interarea planar apsacline, longer than anacline dorsal interarea, delthyrium and notothyrium open ; radial ornamentation fasciocostellate commonly 3 per mm, 5 mm antero-medially of the dorsal umbo, external branches poorly developed in the first three sectors, costellae reflexed postero-laterally, follicular embayments rarely indenting internal surfaces of hinge-line.

Teeth small, supported by dental plates extending anteriorly for 17% of the length of the pedicle valve and extending laterally for 150% of their length ; ventral muscle field elongately oval extending forwards for 38% of the length of the valve with splayed diductor scars almost enclosing a pair of small suboval adductor impressions separated by a low ridge ; adjustor scar located on dental plates.

Cardinal process bilobed, differentiated in adult valves into elongate shaft and expanded myophore, notothyrial platform well developed passing anteriorly into low ridge ; brachiophores triangular in outline with divergent bases extending forward for 17% of the length of the valve, becoming massive in adult valves so that they are, on average, only 84% as long as their lateral spread ; oblique sockets not bounded laterally by fulcral plates ; adductor scars quadripartite extending forward for half the length of the valve.

FIGURED MATERIAL.

	length	width (mm)
External and internal moulds of pedicle valve (BB 35474a, b)	8·0	–
External and internal moulds of brachial valve (BB 35475a, b)	4·0	5·0
External and internal moulds of pedicle valve (BB 35476a, b)	9·0	12·0
Incomplete external and internal moulds of brachial valve (BB 35477a, b)	14·0	–
External and internal moulds of brachial valve (BB 35478a, b)	10·0	12·0
Internal mould of pedicle valve (BB 35479)	11·5	–

HORIZON AND LOCALITIES. Meadowtown Beds : BB 35474, 35475 from loose blocks on rough ground 100 yds south-east of Minicop Farm (Grid Ref. SJ 315018) ; BB 35478 from Bed B in measured section in Meadowtown Quarry (Grid Ref. SJ 312012) ; BB 35479 from Quinton's Quarry in the field 200 yds north-east of Meadowtown Chapel (Grid Ref. SJ 312013). BB 35476, 35477 from exposures in a ploughed field along the strike of Betton Beds occurring 180 yds south-west of a well in the lane-side from Meadowtown to Castle Ring (Grid Ref. SJ 310009).

DISCUSSION. *Tissintia prototypa* was first described from the upper part of the *Didymograptus bifidus* shales of the Llandeilo district (Williams 1953 : 180) and is now known from W. Wales and Builth as well as Shropshire, where it occurs abundantly in the Llanvirn Weston Beds. A good sample from the Weston Beds has been statistically compared with a topotypic assemblage. The comparison shows (Tables 77–85) that there is no difference between the two samples in parameters of the shape of the shell, the disposition and size of internal features, or in the radial ornamentation except for a marginally significant delay in the differentiation of the

3ālā costella. This distinction is not considered important enough to merit systematic recognition so that the species may be regarded as a noteworthy homogeneous, short-ranging stock especially characteristic of the Lower Llanvirn of Britain.

The Llandeilo species *T. immatura* from the Meadowtown Beds is more closely related to *T. prototypa* than was originally thought when the two species were erected. Both species are similar in dorsal outline and the relative sizes of internal features. They differ however in a number of important characters. In *T. immatura* the ribbing is significantly coarser ($p > 0{\cdot}001$) with a suggestion that externally branching ribs are more commonly developed in Sector IV; the growth in relative depth of the pedicle valve is faster ($p < 0{\cdot}001$); and the lateral spread of the brachiophore bases is significantly greater ($0{\cdot}05 > p > 0{\cdot}02$). This last difference reflects not only the more divergent disposition of the brachiophore bases in *T. immatura* but also their excessive thickening by secondary shell accretion in mature stages of growth.

A small sample of *Tissintia* from the Betton Beds of Shelve, although stratigraphically intermediate between the two species, was identical with *T. prototypa* in the key differences. Rib counts per mm, 5 mm antero-medially of the umbones of 2, 3 and 5 brachial valves were 4, 5 and 6; the basic statistics for length (l) and depth (th) of 11 pedicle valves were: $\bar{l}$ (var l) = 7·68 (3·872), $\overline{th}$ (var th) = 1·53 (0·27) and $r = 0{\cdot}909$; and for the length (l) and maximum lateral extension (w) of the brachiophore bases in 11 brachial valves they were: $\bar{l}$ (var l) = 1·15 (0·137), $\bar{w}$ (var w) = 1·11 (0·179) and $r = 0{\cdot}936$. Allometry prevailed in both the deepening of the pedicle valve and the extension of the brachiophores, but neither growth rates nor shape parameters differed significantly from those of *T. prototypa*.

The only other species assigned to the genus is *T. convergens* from the Llandeilo of Morocco (Havlíček 1971 : 51), which appears to differ from the British species, at least, in being relatively more transverse and in possessing smaller brachiophores and longer, more flabellate ventral muscle scars.

TABLE 77

Statistics of length (l) and length of brachiophore bases (lc) in n brachial valves of *Tissintia prototypa* (Williams) from the Weston Beds (A) and the Lower Llanvirn of Llandeilo (B), and of *T. immatura* (Williams) from the Meadowtown Beds (C)

	A	B	C
n	21	55	64
$\bar{l}$ mm (var l)	8·87 (14·326)	8·59 (4·4)	6·03 (14·756)
$\overline{lc}$ mm (var lc)	1·4 (0·303)	1·17 (0·054)	1·05 (0·361)
r	0·941	0·871	0·966
$\overline{\log_e l}$ (var $\log_e l$)	2·0986 (0·1674)	2·122 (0·0578)	1·6267 (0·3404)
$\overline{\log_e lc}$ (var $\log_e lc$)	0·2685 (0·1426)	0·1384 (0·0387)	−0·0903 (0·2824)
r_e	0·944	0·875	0·972
α (var α)	0·9229 (0·00485)	0·8182 (0·00295)	0·9108 (0·00075)

TABLE 78

Statistics of length (l) and length of adductor scars from umbo (sc) in n brachial valves of *Tissintia prototypa* (Williams) from the Weston Beds (A) and the Lower Llanvirn of Llandeilo (B), and of *T. immatura* (Williams) from the Meadowtown Beds (C)

	A	B	C
n	12	6	34
$\bar{l}$ mm (var l)	10·43 (8·345)	11·18 (3·402)	8·08 (15·198)
$\overline{sc}$ mm (var sc)	4·77 (1·599)	5·13 (0·926)	4·04 (2·818)
r	0·935	0·979	0·984
a (var a)	0·4377 (0·00242)	0·5217 (0·0028)	0·4306 (0·00018)

TABLE 79

Statistics of length (l) and maximum width (w) of n brachial valves of *Tissintia prototypa* (Williams) from the Weston Beds (A) and the Lower Llanvirn of Llandeilo (B), and of *T. immatura* (Williams) from the Meadowtown Beds (C)

	A	B	C
n	27	54	52
$\bar{l}$ mm (var l)	6·92 (18·479)	7·62 (9·47)	5·66 (11·628)
$\bar{w}$ mm (var w)	9·01 (29·887)	9·25 (10·229)	7·11 (15·49)
r	0·987	0·903	0·99
$\overline{\log_e l}$ (var $\log_e l$)	1·771 (0·3265)	1·9559 (0·1508)	1·5786 (0·3097)
$\overline{\log_e w}$ (var $\log_e w$)	2·0424 (0·3131)	2·1678 (0·1129)	1·8275 (0·2674)
r_e	0·989	0·91	0·992
α (var α)	0·9793 (0·00464)	0·8653 (0·00247)	0·9292 (0·00027)

TABLE 80

Statistics of length (l) and thickness (th) of n pedicle valves of *Tissintia prototypa* (Williams) from the Weston Beds (A) and the Lower Llanvirn of Llandeilo (B), and of *T. immatura* (Williams) from the Meadowtown Beds (C)

	A	B	C
n	14	31	49
$\bar{l}$ mm (var l)	10·81 (18·219)	7·88 (3·719)	7·18 (12·06)
$\overline{th}$ mm (var th)	2·59 (1·299)	1·45 (0·17)	2·19 (0·925)
r	0·895	0·800	0·932
a (var a)	0·267 (0·00118)	0·2138 (0·00057)	0·277 (0·00022)

TABLE 81

Statistics of length (l) and length of dental plates (dl) in n pedicle valves of *Tissintia prototypa* (Williams) from the Weston Beds (A) and the Lower Llanvirn of Llandeilo (B), and of *T. immatura* (Williams) from the Meadowtown Beds (C)

	A	B	C
n	21	27	53
$\bar{l}$ mm (var l)	11·45 (9·102)	8·36 (3·282)	6·92 (14·129)
$\overline{dl}$ mm (var dl)	1·68 (0·328)	1·06 (0·055)	1·18 (0·341)
r	0·909	0·624	0·946
$\overline{\log_e l}$ (var $\log_e l$)	2·4044 (0·0671)	2·0999 (0·0461)	1·8049 (0·2586)
$\overline{\log_e dl}$ (var $\log_e dl$)	0·4614 (0·1103)	0·0297 (0·0484)	0·0522 (0·2205)
r_e	0·914	0·627	0·952
α (var α)	1·2822 (0·0143)	1·0246 (0·02548)	0·9234 (0·00157)

TABLE 82

Statistics of length (l) and length of ventral muscle scar (sc) in n pedicle valves of *Tissintia prototypa* (Williams) from the Weston Beds (A) and the Lower Llanvirn of Llandeilo (B), and of *T. immatura* (Williams) from the Meadowtown Beds (C)

	A	B	C
n	20	17	43
$\bar{l}$ mm (var l)	11·45 (9·581)	9·51 (2·327)	7·5 (13·902)
$\overline{sc}$ mm (var sc)	4·11 (1·881)	3·31 (0·432)	2·84 (2·991)
$\overline{r}$	0·934	0·729	0·96
$\overline{\log_e l}$ (var $\log_e l$)	2·4023 (0·0706)	2·2392 (0·0255)	1·9048 (0·2208)
$\overline{\log_e sc}$ (var $\log_e sc$)	1·3606 (0·1056)	1·1762 (0·0389)	0·8848 (0·316)
r_e	0·937	0·73	0·967
α (var α)	1·2231 (0·01008)	1·2351 (0·04747)	1·1963 (0·00229)

TABLE 83

Statistics of length (l) and maximum lateral extension (w) of the brachiophore bases of n brachial valves of *Tissintia prototypa* (Williams) from the Lower Llanvirn of Llandeilo (A) and *T. immatura* (Williams) from the Meadowtown Beds (B)

	A	B
n	61	67
$\bar{l}$ mm (var l)	1·22 (0·069)	1·09 (0·382)
$\bar{w}$ mm (var w)	1·1 (0·065)	1·29 (0·441)
$\overline{r}$	0·895	0·927
$\overline{\log_e l}$ (var $\log_e l$)	0·1729 (0·0457)	−0·0527 (0·2783)
$\overline{\log_e w}$ (var $\log_e w$)	0·0707 (0·052)	0·1372 (0·235)
r_e	0·9	0·935
α (var α)	1·0674 (0·00367)	0·919 (0·00163)

TABLE 84

Proportions of the earlier insertion of 10 costellae relative to 10 others (with the number of brachial valves in which both costellae originated at the same growth stage in brackets) for *Tissintia prototypa* (Williams) from the Weston Beds (A) and the lower Llanvirn of Llandeilo (B) and for *Tissintia immatura* (Williams) from the Meadowtown Beds (C)

	A	B	C
$1\bar{a}l$) $1\bar{b}$	1/7 (1)	0/6 (2)	1/4 (2)
$1\bar{b}$) $1a^{\circ}$	8/8	10/13 (1)	5/9 (1)
$2\bar{b}$) $2a^{\circ}$	9/9	15/17 (1)	11/12 (2)
$2\bar{c}$) $2a^{\circ}$	1/3	2/11 (3)	0/4 (1)
$2\bar{a}l$) $2\bar{b}$	1/3 (5)	0/5 (7)	2/8 (3)
$3\bar{a}la$) $3a^{\circ}$	1/4 (4)	0/14	3/14 (1)
$3\bar{c}$) $3a^{\circ}$	2/7 (2)	0/15	1/12 (1)
$3\bar{a}l\bar{a}$) $2a^{\circ}$	8/8	3/10 (2)	9/12
$4\bar{b}$) $4b^{\circ}$	8/8	3/3 (2)	1/4 (3)
$4\bar{a}l^{\circ}$) $4\bar{b}l$	0/2	1/3	2/3

TABLE 85

The distribution of brachial valves of *Tissintia prototypa* (Williams) from the Weston Beds (A) and the Lower Llanvirn of Llandeilo (B), and of *Tissintia immatura* (Williams) from the Meadowtown Beds (C), with 3–6 costellae per mm, 5mm antero-medially of the dorsal umbones

	costellae per mm			
	3	4	5	6
A	1	4	11	0
B	2	18	27	4
C	12	6	1	0

Family **LINOPORELLIDAE** Schuchert & Cooper 1931

SALOPIA Williams 1955

Salopia cf. ***salteri*** (Davidson)

(Pl. 19, figs. 10, 11)

An incomplete mould of a brachial valve (BB 35426a, b) is the only record of *Salopia* in Spy Wood Grit. The specimen, which was recovered from the outcrops 1100 yds NNE of Rorrington (Grid Ref. SJ 303015), indicates that the convex and gently sulcate valve was about 5 mm long and was ornamented by fine multicostellae with a density of 6 per mm at the antero-medial margin. Although the mould is broken posteriorly it is possible to determine that the cardinalia included a pair of widely placed brachiophore bases bounding a low notothyrial platform supporting the linear shaft of a cardinal process. The notothyrial platform passes anteriorly into a broad median ridge with adductor impressions on either side.

In respect of its preserved features, the valve is indistinguishable from that of *Salopia salteri* (Davidson) as illustrated in Whittington & Williams (1955, pl. 38, figs. 45, 46) and provisionally, at least, may be assigned to that species.

Salopia sp.

(Pl. 19, figs. 6–9)

In contrast to the Spy Wood representative of *Salopia*, the three congeneric moulds from the Whittery Shales, exposed in Whittery Quarry (BB 35428a, b, BB 35429a, b) at the south end of Whittery Wood near Chirbury (Grid Ref. SO 275981) and in the stream (BB 35430a, b) at the north end of Spring Coppice 865 yds south-east of Hockleton Bridge (Grid Ref. SO 279997), are less decisively related to *S. salteri*. The two pedicle valves represented by the moulds BB 35429 and 35430 were strongly convex, about one-quarter as deep as long, rectimarginate, with a high apsacline interarea. The widely placed dental plates were more nearly parallel in the smaller valve than the larger although the muscle fields of both, consisting of a pair of lobate diductor scars flanking a narrow median adductor track, were impressed beyond the limits of the dental plates and extended forwards for up to one-third the length of the valve. The ribbing was too poorly preserved on external moulds to indicate more than a finely costellate condition. However, costellae ornamenting the brachial valve (BB 35428), although occurring with a density comparable with that of

S. salteri of 5 per mm, 5 mm antero-medially of the umbo, are sharper and less uniformly multicostellate. This difference is the only important one observed because the apparent greater convexity and sulcation are attributable to post-diagenetic deformation of the specimen. When more is known about ribbing variation in *Salopia* the difference may prove to have no systematic status ; meanwhile it seems advisable not to allocate the specimens to any described species.

Suborder CLITAMBONITIDINA Öpik 1934

Superfamily **GONAMBONITACEA** Schuchert & Cooper 1931

Family **GONAMBONITIDAE** Schuchert & Cooper 1931

Subfamily **ANOMALORTHINAE** Ulrich & Cooper 1936

OSLOGONITES Öpik 1939

Oslogonites ? sp.

(Pl. 19, figs. 12, 13)

An external and incomplete internal mould of a brachial valve (BB 35326a, b) about 2 mm long and 3·5 mm wide, from the Mytton Flags exposed along the side of the footpath at road level, 1100 yds NNW of Wood House (Grid Ref. SJ 338003), is believed to represent the remains of an immature specimen of *Oslogonites* Öpik. The valve was semicircular in outline and evenly concave in profile with acute cardinal angles. It was ornamented by intercalated costellae, numbering 6 per mm anteriorly, with every fourth or fifth thickened to delineate a series of sectors in an unequally parvicostellate fashion. Enough of the internal mould is preserved to show that the socket ridges were acutely disposed to the hinge-line to define narrow sockets and joined medially in a small ridge which was not differentiated into a cardinal process. There was no notothyrial platform nor median ridge, but a pair of curved septa occurred in the area normally occupied by adductor scars.

The concavity of the brachial valve and the unequally parvicostellate nature of its radial ornamentation suggest either a strophomenidine or a clitambonitidine affinity. However, the disposition of the socket ridges favour its identification as a clitambonitidine ; and since the anomalous lack of a notothyrial platform may be attributable to the immaturity of the valve, the specimen is best assigned to *Oslogonites*. In fact the Shelve brachial valve probably resembled that of *Oslogonites costellatus* (Öpik 1939 : 134) from the Arenigian *expansus* Shale of Norway except that it was more concave and its parvicostellate ornamentation more strongly differentiated into sectors.

Family **KULLERVOIDAE** Öpik 1934

KULLERVO Öpik 1932

Kullervo sp.

(Pl. 19, figs. 14, 15)

The only kullervoidid represented in the Whittard collection consists of a fractured internal mould and an incomplete complementary external mould of a pedicle valve (BB 35340a, b) from the Meadowtown Beds exposed in the lane to Waitchley 140 yds north of Meadowtown Chapel (Grid Ref. SJ 311014). These meagre fragments indicate that the valve was about 4·0 mm long, 5·5 mm wide and 1·5 mm deep with a high apsacline interarea, slightly acute cardinal angles and a faint antero-medial sulcus. Radial ornamentation consisted of about 20 rounded costae and a few costellae arising by branching with 3 ribs per mm at the antero-lateral margin. The ribs and interspaces were crossed by strong, outwardly deflected lamellae. This concentric ornamentation is regularly arranged with a density of 4 lamellae per mm at the valve margin and breaks the continuity of the ribs. The valve interior was dominated by a spondylium supported by a median septum extending forward for 1·5 mm.

Consideration of the valve profile and outline, ornamentation, and the nature of the spondylial support, suggests that the specimen is best assigned to *Kullervo*. Indeed, sufficient radial ornamentation is preserved to prompt comparison with one of the earliest recorded species, *K. panderi* (Öpik 1934 : 164) from the C_2 horizon of Estonia, because there is no strong differentiation between the postero-lateral and medial sectors of radial ornamentation as in later species. However, until more material is obtained to assess the validity of this comparison, only a generic identification is appropriate.

Suborder TRIPLESIIDINA Moore 1952

Superfamily **TRIPLESIACEA** Schuchert 1913

Family **TRIPLESIIDAE** Schuchert 1913

TRIPLESIA Hall 1859

Triplesia sp.

(Pl. 19, fig. 16)

An incomplete internal mould (BB 35408), with fragments of the shell adhering, of the genus *Triplesia* have been recovered from the Whittery Shales exposed in the stream at the north end of Spring Coppice, 865 yds south-east of Hockleton Bridge (Grid Ref. SO 279997). The mould is that of a pedicle valve which was 12·5 mm long, 10 mm wide and 2·5 mm deep laterally. Its outline was subquadrate with rounded obtuse cardinal angles and it was indented medially by a strong flat-bottomed sulcus, about half as wide as the maximum width of the valve, which was sharply bent into a right angle to project dorsally as a tongue about one-third as long as the ventral length of the valve. The apsacline interarea, which was curved, bore a medially folded pseudodeltidium, and the external surface bore only fine overlapping lamellae numbering about 14 per mm anteriorly. Internally the dental plates were acutely divergent, extending forward for about one-fifth the length of the valve, while the diductor scars were lightly impressed for over half the length of the valve on either side of a low median ridge.

The Whittery *Triplesia* with its flat-bottomed sulcus and sharply bent, dorsally projecting tongue is immediately distinguishable from penecontemporaneous

European and African species, such as *T. simplex* from the Ktaoua Formation of Morocco (Havlíček 1971 : 66) and *T. deformata* (Barrande 1879) from the Zahofany Formation of Czechoslovakia (Havlíček 1950 : 89), with their gently rounded non-geniculate sulci. It is, however, similar to *T. subcarinata* (Cooper 1956 : 538) from the Lebanon Formation of Tennessee ; but systematic consideration of this apparent relationship must await the information provided by more material.

BICUSPINA Havlíček 1950

Bicuspina subquadrata sp. nov.

(Pl. 19, figs. 17–19 ; Pl. 20, figs. 1, 2)

DIAGNOSIS. Subquadrate *Bicuspina*, with a dorsal fold about 44% as wide as the brachial valve length, usually bearing a median costa which rarely branches within 5 mm of the umbo, finely lamellose with 7 lamellae developed between 5 and 6 mm antero-medially of the umbo.

DESCRIPTION. Medium-sized, dorsibiconvex, subquadrate *Bicuspina* with rounded, obtuse cardinal angles ; pedicle valve 25% as deep as long with flat-bottomed median sulcus bounded by parallel sides and evenly convex flanks ; brachial valve 65% as long as wide and 37% as deep as long with a strong median fold 44% as wide as the valve is long ; ventral interarea curved apsacline, pseudodeltidium with narrow median fold, dorsal interarea vestigial ; radial ornamentation of rounded ribs with a mean wavelength of 0·44 mm (variance 0·02), 5 mm anterior of the umbones of 15 brachial valves—a median costa (flanked by 2 laterals) occurs on folds of 11 out of 16 brachial valves and bifurcates within 5 mm of the umbo in only 1 valve—9 to 15 ribs occur on the flanks of brachial valves between 5 and 7·5 mm long ; concentric ornamentation of delicate overlapping lamellae with 6 or 7 occurring between 5 and 6 mm anteriorly of the umbones of 2 and 7 brachial valves respectively.

Pedicle tube relatively short, averaging 12% the length of the pedicle valve and with slightly curved pedicle passage ; rounded teeth supported by acutely divergent dental plates 60% as long as their anterior separation and extending forward for 17% of the length of the valve ; suboval muscle field well impressed in late adult stages of growth only, extending forward for 48% of the length of the pedicle valve and consisting of a short median adductor and a pair of ventral adjustors situated on either side of the internal opening of the pedicle tube, which is flanked by long diductor scars.

Cardinalia consisting of forked, posteriorly curving cardinal process, and short, acutely divergent, pointed brachiophores ; sockets disposed parallel to the hinge-line, extending laterally for 33% of the length of the valve, not restricted distally by ridges of secondary shell.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	Internal and incomplete external moulds of pedicle valve (BB 35480a, b)	18·0	20·0

		length	width (mm)
Paratypes	External and internal moulds of brachial valve (BB 35481a, b)	11·5	–
	External and incomplete internal moulds of pedicle valve (BB 35482a, b)	12·0	16·5
	Internal mould of brachial valve (BB 35483)	14·5	22·5

Horizon and localities. Whittery Shales: BB 35480 from Tuffaceous Shale exposed in the lower part of the western bank of the River Camlad 60 yds north-east of Marrington Farm (Grid Ref. SO 272970); other specimens from Whittery Quarry at the south end of Whittery Wood near Chirbury (Grid Ref. SO 275981).

Bicuspina modesta sp. nov.

(Pl. 20, figs. 3–8)

Diagnosis. Subquadrate *Bicuspina* with a dorsal fold about half as wide as the valve length, commonly bearing a median costa which usually branches within 5 mm of umbo, lamellose with 5 lamellae developed between 5 and 6 mm antero-medially.

Description. Small, biconvex, subquadrate *Bicuspina* with obtuse or, more rarely, orthogonal cardinal angles; pedicle valve 24% as deep as long with a flat-bottomed median sulcus bounded by parallel sides and evenly convex flanks, brachial valve 75% as long as wide and 35% as deep as long with a splayed median fold 50% as wide as the valve is long; ventral interarea curved apsaline, pseudodeltidium with narrow median fold, dorsal interarea vestigial; radial ornamentation of rounded ribs with a mean wavelength of 0·5 mm (variance 0·08), 5 mm anterior of the umbones of 27 brachial valves, median costa (flanked by 2 laterals) occurs on folds of 34 out of 37 brachial valves and bifurcates within 5 mm of the umbones of 19 valves; 11 to 17 ribs occur on the flanks of brachial valves between 5 and 7·5 mm long; concentric ornamentation of overlapping lamellae with 4 or 5 occurring between 5 and 6 mm anteriorly of the umbones of 2 brachial valves in each case.

Pedicle tube and passage averaging 11% of the length of the pedicle valve; small teeth supported by acutely divergent dental plates extending forward for 68% of their anterior separation and 15% as long as the valve; muscle field poorly impressed extending forward for 55% of the length of the pedicle valve.

Cardinalia consisting of forked posteriorly curving cardinal process and short, acutely divergent, pointed brachiophores; sockets disposed parallel to the hinge-line extending laterally for 26% of the length of the valve, usually defined distally by ridges of secondary shell.

Type material.

		length	width (mm)
Holotype	External and internal moulds of pedicle valve (BB 35510a, b)	10·0	12·0
Paratypes	External and internal moulds of brachial valve (BB 35511a, b)	7·0	8·5
	External and internal moulds of brachial valve (BB 35512a, b)	9·5	11·5

HORIZON AND LOCALITY. Spy Wood Grit exposed 1100 yds north-east of Rorrington (Grid Ref. SJ 303015).

DISCUSSION. *Bicuspina* is well represented in the Spy Wood Grit and the Whittery Shales by two closely related forms which are, nonetheless, distinguishable in the relative size of the median fold and sulcus and in ornamentation. As comparison of growth axes demonstrated (Tables 86–93), the two species are alike in the outline and depth of the valves as well as in the relative growth of dental plates and cardinalia. The dorsal fold of *B. subquadrata*, however, is relatively narrower than that of *B. modesta*, and a *t*-test indicates that the difference was maintained during shell growth at a significant level ($0{\cdot}01 > p > 0{\cdot}001$). This difference may have influenced the incidence of ribs on the folds because a median costa is more frequently absent or, if present, more likely to have bifurcated in later stages of shell growth in *B. subquadrata* than in *B. modesta*. Concentric lamellae of the former species are also more delicate and more closely spaced than those of *B. modesta*.

The Shelve species may be ancestral to *B. spiriferoides* (M'Coy) which is widely distributed in late Soudleyan and Longvillian rocks of Shropshire and N. Wales. Lack of suitable material has precluded study of the variability of the radial ornament and especially the development of a dorsal median costa (Williams 1963 : 426). *B. spiriferoides*, however, is distinct in its relatively greater width, its rectangular to acute cardinal angles, and its relatively long dental plates and ventral muscle field.

The *Bicuspina* described by Havlíček (1950 : 88–90) from the late Llandeilian–early Caradocian (Chrustenice and Lodeňice substages) rocks of Czechoslovakia also differ in a number of respects but especially in the relative coarseness of ribbing in *B. cava* (Barrande) and the lack of fold and sulcus in *B. multicostellata* Havlíček.

TABLE 86

Statistics of length (l) and maximum width (w) of n brachial valves of *Bicuspina subquadrata* sp. nov. (A) and *Bicuspina modesta* sp. nov. (B)

	A	B
n	7	34
$\bar{l}$ mm (var l)	9·10 (10·037)	6·55 (8·024)
$\bar{w}$ mm (var w)	13·94 (19·843)	8·70 (13·113)
r	0·986	0·966
a (var a)	1·4061 (0·01130)	1·2783 (0·03384)

TABLE 87

Statistics of length (l) and maximum depth (th) of n brachial valves of *Bicuspina subquadrata* sp. nov. (A) and *Bicuspina modesta* sp. nov. (B)

	A	B
n	10	33
$\bar{l}$ mm (var l)	8·13 (4·447)	6·70 (7·165)
$\overline{th}$ mm (var th)	3·00 (1·315)	2·36 (1·033)
r	0·916	0·869
a (var a)	0·5439 (0·00595)	0·3797 (0·00114)

TABLE 88

Statistics of length (l) and maximum width of folds (f) in n brachial valves of *Bicuspina subquadrata* sp. nov. (A) and *Bicuspina modesta* sp. nov. (B)

	A	B
n	10	36
$\bar{l}$ mm (var l)	8·55 (5·660)	6·41 (3·757)
$\bar{f}$ mm (var f)	3·79 (2·465)	3·18 (0·747)
r	0·9537	0·794
$\overline{\log_e l}$ (var $\log_e l$)	2·1086 (0·0746)	1·8143 (0·0875)
$\overline{\log_e f}$ (var $\log_e f$)	1·2533 (0·1583)	1·1205 (0·0714)
r_e	0·958	0·8000
α (var α)	1·4567 (0·02400)	0·9033 (0·00886)

TABLE 89

Statistics of length (l) and maximum depth (th) of n pedicle valves of *Bicuspina subquadrata* sp. nov. (A) and *Bicuspina modesta* sp. nov. (B)

	A	B
n	13	19
$\bar{l}$ mm (var l)	9·82 (14·945)	7·12 (2·352)
$\overline{th}$ mm (var th)	2·46 (1·382)	1·68 (0·335)
r	0·949	0·807
a (var a)	0·3042 (0·00083)	0·3774 (0·00292)

TABLE 90

Statistics of length (l) and length of dental plates (dl) in n pedicle valves of *Bicuspina subquadrata* sp. nov. (A) and *Bicuspina modesta* sp. nov. (B)

	A	B
n	12	32
$\bar{l}$ mm (var l)	10·47 (13·713)	7·33 (3·207)
$\overline{dl}$ mm (var dl)	1·77 (0·858)	1·13 (0·092)
r	0·925	0·524
$\overline{\log_e l}$ (var $\log_e l$)	2·2903 (0·1178)	1·9637 (0·0578)
$\overline{\log_e dl}$ (var $\log_e dl$)	0·4476 (0·2430)	0·0916 (0·0690)
r_e	0·936	0·533
α (var α)	1·4363 (0·02974)	1·0927 (0·02640)

TABLE 91

Statistics of length (dl) and anterior separation (dw) of dental plates in n pedicle valves of *Bicuspina subquadrata* sp. nov. (A) and *Bicuspina modesta* sp. nov. (B)

	A	B
n	12	33
$\overline{dl}$ mm (var dl)	1·59 (0·444)	1·15 (0·076)
$\overline{dw}$ mm (var dw)	2·66 (1·284)	1·68 (0·122)
r	0·905	0·647
a (var a)	1·7000 (0·05245)	1·2679 (0·03014)

TABLE 92

Statistics of length (l) and length (tl) of pedicle tubes in n pedicle valves of *Bicuspina subquadrata* sp. nov (A) and *Bicuspina modesta* sp. nov. (B)

	A	B
n	10	24
$\bar{l}$ mm (var l)	11·39 (11·677)	7·54 (3·423)
$\overline{tl}$ mm (var tl)	1·41 (0·668)	0·85 (0·215)
r	0·865	0·434
$\overline{\log_e l}$ (var $\log_e l$)	2·3897 (0·0862)	1·9907 (0·0584)
$\overline{\log_e tl}$ (var $\log_e tl$)	0·1988 (0·2896)	0·2927 (0·2603)
r_e	0·887	0·457
α (var α)	1·8330 (0·10570)	2·1112 (0·16440)

TABLE 93

Statistics of length (l) and lateral extension of sockets (br) in n brachial valves of *Bicuspina subquadrata* sp. nov. (A) and *Bicuspina modesta* sp. nov. (B)

	A	B
n	7	17
$\bar{l}$ mm (var l)	10·21 (10·858)	7·46 (8·487)
$\overline{br}$ mm (var br)	3·37 (0·930)	1·95 (0·596)
r	0·887	0·905
a (var a)	0·2927 (0·00365)	0·2650 (0·00084)

CAEROPLECIA gen. nov.

NAME. A triplesiid with a concentric ornament like the end threads (Gk. *καῖρος*) in a loom.

DIAGNOSIS. Subcircular, dorsibiconvex, uniplicate triplesiids with a strongly convex brachial valve and a gently convex to flat pedicle valve, bearing respectively a flat-topped fold and complementary sulcus arising anterior of the umbo ; ventral interarea short, apsacline, pseudodeltidium narrowly folded medially, foramen supra-apical, dorsal interarea linear ; radial ornamentation of coarse costae and branching costellae originating during later stages of shell growth, concentric ornamentation of delicate rounded ridges (fila).

Ventral interior with variably developed pedicle tube, small teeth supported by short acutely divergent dental plates, muscle scars broadly bilobed with low median ridge dividing narrow adductor band ; mantle canal pattern unknown.

Dorsal interior with short forked cardinal process, divergent rod-like brachiophores, and small oblique sockets ; fine median ridge dividing quadripartite adductor scars with anterior pair larger than posterior ; mantle canal pattern unknown.

TYPE SPECIES. *Caeroplecia plicata* sp. nov. from the Whittery Shales, Shropshire.

DISCUSSION. The new genus is unique among triplesiaceans in being concentrically ornamented by fine, rounded ridges instead of overlapping lamellae. The delayed development of radial ornamentation, the subcircular outline and the flattish pedicle valve together also distinguish *Caeroplecia* from all other triplesiid genera.

Caeroplecia plicata sp. nov.

(Pl. 20, figs. 14–16 ; Pl. 21, figs. 1–6, 8 ; Text-fig. 9)

DIAGNOSIS. Subcircular *Caeroplecia* with a brachial valve about 80% as long as wide, and low rounded costellae with a wavelength of 0·6 mm, 5 mm antero-medially of the dorsal umbo, first appearing on shells more than 3 mm long and commonly numbering 6 on the fold and 5 to 9 on the lateral slopes.

DESCRIPTION. Dorsibiconvex, subcircular *Caeroplecia* with obtusely rounded cardinal angles ; pedicle valve 18% as deep as long with flat-bottomed shallow median sulcus and flattened lateral slopes ; brachial valve 80% as long as wide and 30% as deep as long with flat median fold, 43% as wide as the length of the valve, originating 2·5 mm anterior of umbo (average for 4 brachial valves) ; ventral interarea short apsacline, pseudodeltidium narrowly folded medially, dorsal interarea linear ; concentric ornamentation of 8 to 10 fila per mm between 5 and 6 mm anterior of dorsal umbo, radial ornamentation not developed on immature shells up to an average of 3·2 mm long (variance 2·233 for 10 brachial valves), thereafter rounded costae and implanted costellae occur, having a mean wavelength of 0·63 mm, 5 mm anterior of the umbones of 4 brachial valves with 5, 6, 7 and 8 ribs on the folds of 2, 3, 1 and 2 brachial valves between 9 and 12 mm long and 5 to 9 ribs on the lateral slopes.

Pedicle tube weakly developed, less than 7% as long as the valve ; teeth supported by acutely divergent dental plates extending anteriorly for a mean of 11·8% of the length of 6 pedicle valves (variance 5·86) ; muscle field faintly impressed but broadly bilobed, extending anteriorly for about one-third the length of the valve, with splayed diductor scars not enclosing a narrow parallel-sided adductor track divided by a fine median ridge.

Cardinalia consisting of slightly recurved forked cardinal process, short brachiophores and obliquely placed sockets arranged along the hinge-line for an average of 24% of the length of 5 brachial valves ; adductor scars quadripartite, lightly impressed about a fine median ridge.

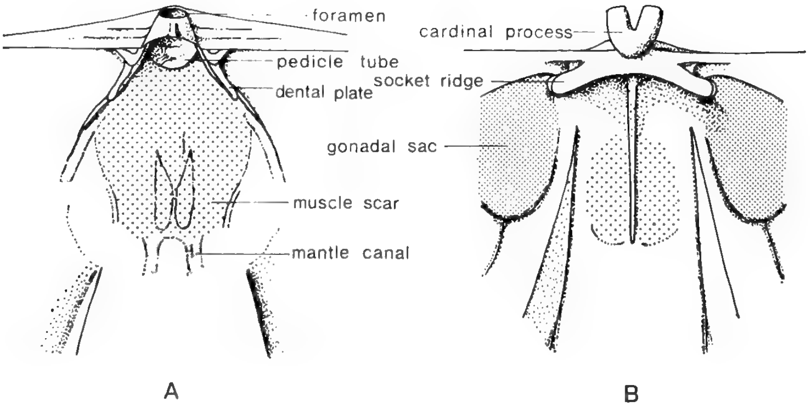


FIG. 9. Diagrammatic views of (A) the ventral and (B) the dorsal interiors of *Caeroplecia*.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	External and internal moulds of pedicle valve (BB 35342a, b)	9·3	11·2
PARATYPES	Partly exfoliated pedicle valve with internal mould (BB 35343a, b)	12·0	–
	Internal mould of pedicle valve (BB 35344)	11·5	14·5
	Incomplete external and internal moulds of brachial valve (BB 35345a, b)	–	–
	External and internal moulds of pedicle valve (BB 35346a, b)	10·0	–
	Incomplete external and internal moulds of pedicle valve (BB 35347a, b)	–	–
	External and internal moulds of brachial valve (BB 35348a, b, c)	12·5	13·5
	External and internal moulds of brachial valve (BB 35349a, b)	12·2	15·5
	External and internal moulds of brachial valve (BB 35350a, b)	6·5	7·5
	Incomplete external and internal moulds of brachial valve (BB 35351a, b)	–	–

TYPE HORIZON AND LOCALITIES. Whittery Shales: BB 35343 and 35347 from exposures in the stream at the north end of Spring Coppice, 865 yds south-east of Hockleton Bridge near Chirbury (Grid Ref. SO 279997); BB 35350 from exposures in the lower part of the west bank of the River Camlad 60 yds north-east of Marrington Farm (Grid Ref. SO 272970); all other specimens from Whittery Quarry at the south end of Whittery Wood near Chirbury (Grid Ref. SO 275981).

DISCUSSION. One Welsh species, *Oxoplecia mutabilis* Williams (in Whittington & Williams 1955 : 411), and possibly two American forms, the Porterfield *O. gibbosa* and the Trenton *O. pennsylvanica* (Cooper 1956 : 543, 553) can be assigned to *Caeroplecia*, although the presence in the two latter species of the ridge-like concentric ornamentation so characteristic of the genus has still to be demonstrated. However, all three differ in the number of ribs on the fold, *C. mutabilis* having a greater number (6 to 12, usually 9) and the American species significantly fewer (3 or 4). *C. mutabilis*, which is probably the most closely related, also differs in being relatively wider and in having grown to lengths of 7 or 8 mm before comparatively fine costae and costellae, with a wavelength of 0·3 to 0·5 mm, appear.

TABLE 94

Statistics of length (l) and maximum width (w) of 7 brachial valves of *Caeroplecia plicata* gen. et sp. nov.

$\bar{l}$ mm (var l)	9·81 (10·558)
$\bar{w}$ mm (var w)	12·31 (17·092)
r	0·995
a (var a)	1·2724 (0·00311)

TABLE 95

Statistics of length (l) and maximum depth (th) of 7 brachial valves of *Caeroplecia plicata* gen. et sp. nov.

$\bar{l}$ mm (var l)	9·81 (10·558)
$\overline{th}$ mm (var th)	2·89 (2·381)
r	0·865
a (var a)	0·4749 (0·01136)

TABLE 96

Statistics of length (l) and maximum width of the folds (f) in 6 brachial valves of *Caeroplecia plicata* gen. et sp. nov.

$\bar{l}$ mm (var l)	9·48 (10·686)
$\bar{f}$ mm (var f)	4·12 (2·322)
r	0·952
a (var a)	0·4661 (0·00509)

TABLE 97

Statistics of length (l) and maximum depth (th) of 10 pedicle valves of *Caeroplecia plicata* gen. et sp. nov.

$\bar{l}$ mm (var l)	11·45 (5·679)
$\overline{th}$ mm (var th)	2·02 (0·409)
r	0·636
a (var a)	0·2683 (0·00535)

OXOPLECIA Wilson 1913

1913 *Oxoplecia* Wilson : 81.

The distinction between *Oxoplecia* and *Bicuspina* is finely drawn. Ignoring the variability normally inherent to the development of a fold and sulcus, and radial and concentric ornamentation, the difference ultimately rests on the spiriferoid outline and pedicle tube of *Bicuspina* (Wright in Williams *et al.* 1965 : H358). These features are likely to have arisen by a lateral acceleration in the growth of the cardinal margins and secondary shell accretion around the internal opening of the pedicle foramen respectively, and were not always equally developed in stratigraphically earlier stocks. Thus Llandeilian *Bicuspina* of Czechoslovakia (Havlíček 1950 : 18–19) are strongly orthoid in outline, and contemporaraneous *Oxoplecia* from S.W. Wales have incipient pedicle tubes (R. Addison, pers. comm.). In effect it is likely that members of the earlier-occurring and longer-ranging cosmopolitan *Oxoplecia* were ancestral to *Bicuspina*, which appears to be restricted to the Llandeilian and Caradocian rocks of Europe. It is even possible that the species described below is more closely related to *Bicuspina* than contemporaneous American *Oxoplecia* which are typically elliptical in outline, strongly uniplicate, lamellose and coarsely costellate.

***Oxoplecia* cf. *nantensis* MacGregor**

(Pl. 20, figs. 9–13)

1961 *Oxoplecia nantensis* MacGregor : 196.

Diagnosis. Subcircular, subequally biconvex *Oxoplecia* with a variably developed dorsal fold over half as wide as the brachial valve length, and fine radial ornament consisting of ribs averaging 0·3 mm in wavelength, 5 mm antero-medially of dorsal umbo.

Description. Small, subequally biconvex *Oxoplecia* with obtuse cardinal angles and a hinge-line about three-quarters the maximum width of the shell; pedicle valve 23% as deep as long with rounded variably defined sulcus, brachial valve 84% as long as wide and 29% as deep as long with a broadly rounded fold 57% as wide as the brachial valve is long; ventral interarea curved apsacline, pseudodeltidium with narrow median fold, dorsal interarea linear; up to 10 rounded branching ribs, usually not including a median costa and with a mean wavelength of 0·31 mm, 5 mm anterior of the umbones, occur on the folds and 10 to 12 ribs on the flanks of 5 brachial valves less than 10 mm long; concentric ornamentation of overlapping lamellae numbering about 7 between 5 and 6 mm anterior of the dorsal umbo.

Pedicle passage 5% as long as the pedicle valve, rarely with incipient traces of pedicle tube, small teeth supported by acutely divergent dental plates extending forward for 11% the length of the valve; muscle field unknown.

Cardinalia consisting of deeply bilobed cardinal process and short brachiophores, simple sockets arranged parallel to the hinge-line and extending laterally for almost one-quarter the length of the valve.

Figured material.

	length	width (mm)
External and internal moulds of pedicle valve (BB 35320a, b)	8·0	8·5
Incomplete internal mould of brachial valve (BB 35321)	6·0	8·0
External and internal moulds of brachial valve (BB 35322a, b)	8·5	9·5
Incomplete internal mould of brachial valve (BB 35323)	–	–

Horizon and localities. Meadowtown Beds: BB 35322 from exposures along the lane to Lower Ridge from bench mark 754, Little Weston (Grid Ref. SO 293984); the remaining specimens from temporary exposures at the side of a cart-track near Waitchley (Grid Ref. SJ 311018).

Discussion. *Oxoplecia* is fairly widely distributed throughout the Lower Llandeilo rocks of Wales and Shropshire but is never common in any one locality so that data about its morphological variability are not abundant. It is, however, immediately distinguishable from penecontemporaneous *Oxoplecia* from other regions in the variable development of the fold and sulcus and especially in the fineness of the radial ornamentation. This is true even of the most closely comparable American species, the Chazyan *Oxoplecia costellata* (Cooper 1956 : 540), which further differs in the late development of fold and sulcus. The few *Oxoplecia* species reported from Ordovician successions of Eurasia also differ in other attributes. *Oxoplecia sibirica*, from the Mangaseya Stage of the Siberian platform

(Nikiforova & Andreeva 1961 : 200), is additionally *Onychoplecia*-like in outline and even more finely ribbed ; while the species described by Öpik (1930 : 200) as *'Cliftonia' dorsata* Hisinger may prove to be a *Bicuspina* (Rõõmusoks 1970 : **121**) rather than an *Oxoplecia*.

The Shelve specimens have been assigned to *Oxoplecia nantensis* MacGregor based upon material from the Upper Llandeilo of the Berwyn Hills despite the fact that measurements (MacGregor 1961 : 196) indicate the type specimens at least to be very much wider. The significance of this difference cannot be ascertained until more is known about the variability of shell outline. MacGregor's description of *O. nantensis* also suggests that the Shelve specimens have a greater number of ribs on the fold. However a photograph of the holotype (*Ibid.* pl. 20, fig. 18) shows 6 ribs on the fold in contradiction to an error in description which speaks of '3–5 ribs on the dorsal fold' (*Ibid.* : 197) ; it is possible that modal rib densities for the Shelve and Berwyn *Oxoplecia* do not greatly differ.

Order STROPHOMENIDA Öpik 1934

Suborder STROPHOMENIDINA Öpik 1934

Superfamily **PLECTAMBONITACEA** Jones 1928

Family **LEPTESTIIDAE** Öpik 1933

Subfamily **LEPTESTIINAE** Öpik 1933

PALAEOSTROPHOMENA Holtedahl

Palaeostrophomena sp.

(Pl. 21, figs. 7, 10, 11, 13)

DIAGNOSIS. Semicircular *Palaeostrophomena* just over half as long as wide, ornamented by unequally developed parvicostellae numbering 8 to 10 per mm, 5 mm antero-medially of the umbo, very fine fila and about 8 impersistently concentric rugae ; ventral muscle scar bilobed divided by divergent *vascula media*.

DESCRIPTION. Semicircular *Palaeostrophomena*, with a pedicle valve 53% as long as wide, acute cardinal angles and a very gently concavo-convex profile flattening or slightly resupinate peripherally ; shell surface ornamented by very fine crowded fila, about 8 concentric rugae with a wavelength of about 0·2 mm strongly developed at acute angles to the hinge-line but becoming subdued anteriorly, and by parvicostellae numbering 8 to 10 per mm, 5 mm antero-medially of the umbo, and divided into narrow sectors by accentuated ribs, 10 or 11 of which arise early in the umbonal area ; ventral and shorter dorsal interareas apsacline and anacline respectively with a small pseudodeltidium and a supra-apical foramen, and a dorsal notothyrium filled by a median ridge representing the posterior surface of a plectambonitacean cardinal process.

Ventral interior with relatively small simple teeth, vestigial dental plates and a bilobed ventral muscle scar extending forward for about one-fifth the length of the valve and about three-fifths as long as wide ; diductor scars extending beyond the median adductor impression divided by divergent *vascula media*. Dorsal interior unknown.

FIGURED MATERIAL.

	length	width (mm)
External and internal moulds of pedicle valve (BB 35415a, b)	8·0	14·0
External and internal moulds of pedicle valve with adherent shell (BB 35451a, b)	10·5	–
External moulds of shell (BB 35414a, b)	7·5	14·0

HORIZON AND LOCALITIES. Whittery Shales: BB 35415 from exposures half-way down path below Marrington Farm going southwards (Grid Ref. SO 272967); BB 35451 from the lower part of the succession in the west bank of the River Camlad, 60 yds north-east of Marrington Farm (Grid Ref. SO 272970); BB 35414 from Whittery Quarry at the south end of Whittery Wood near Chirbury (Grid Ref. SO 275981).

DISCUSSION. Despite the apparent absence of accessory teeth in the pedicle valve and the lack of information about the dorsal interior, a few strophomenide moulds recovered from the Whittery Shales may be safely assigned to *Palaeostrophomena* in the wider interpretation of that genus (Williams in Whittington & Williams 1955: 415). In known characteristics, the specimens compare closely with *P. magnifica* from the Derfel Limestone of N. Wales as well as certain Scottish species from the Ardmillan Series of Scotland (Williams 1962: 158), so that specific identification is not possible until more material is available.

Family **EOCRAMATIIDAE** nov.

DIAGNOSIS. Plectambonitaceans (?) with a complementary pseudodeltidium and chilidium, a small submesothyridid foramen, unsupported simple teeth, strong narrowly divergent chilidial plates (?) filling the notothyrium in place of a discrete platform and continuous with widely splayed cup-shaped socket ridges; shell impunctate.

DISCUSSION. There are many features of the new genus *Eocramatia* that reflect the tendency of related major groups to show morphological convergence as they are traced back towards their common ancestry. The presence of a pseudodeltidium and chilidium indicates affinities with the Clitambonitidina, Strophomenidina and Billingsellacea. But the absence of dental plates and the structure of the cardinalia preclude assignment of the genus to the Clitambonitidina, and although the impunctate condition of the shell and the morphology of the pedicle valve suggest that *Eocramatia* was derived from the billingsellaceans, many dorsal features contradict this interpretation. These include the absence of an orthide notothyrial platform, and the nature of the divergent plates filling the notothyrium and their relationship to the socket ridges. In all, then, it seems that it can be fairly confidently assigned to the Strophomenidina.

Although only plectambonitaceans are currently known to have been contemporaneous with *Eocramatia*, representatives of the other two strophomenidine superfamilies, the Strophomenacea and Davidsoniacea, first occur in the Upper Llanvirn and basal Caradoc respectively and are stratigraphically eligible for consideration as related stocks. From a general morphological viewpoint the pseudopunctate strophomenaceans are unlikely to be related, but whether the new genus should be assigned to the plectambonitaceans or the davidsoniaceans mainly depends on the interpretation of the plates filling the notothyrium. These structures are like the chilidial plates of the leptellids and, in conjunction with the planar brachial valve and the absence of a notothyrial platform, suggest that the new genus is a plectambonitacean. On the other hand, the posterior surfaces of the plates appear to have been grooved in life and, therefore, may have functioned as supports for the dorsal diductor muscle bases which were, in contrast, attached to the notothyrial floor between the chilidial plates in plectambonitaceans. If this were so the plates are homologous with the bilobed cardinal process and, together with the impunctate shell condition and simple teeth, hint at a davidsoniacean relationship. The principal features refuting this interpretation are the attitude of the socket ridges, the absence of dental plates and the planar brachial valve ; and, since simple teeth without flanking accessory processes and an impunctate shell are known to have persisted among the most primitive plectambonitaceans such as the contemporaneous plectambonitids and taffiids, it seems more appropriate to assign *Eocramatia* to the Plectambonitacea at least until better preserved material is available to decide the issues in question.

Having had so much difficulty in assigning *Eocramatia* to a superfamily it is not surprising to find that its familial connections within that taxon are at present elusive. In some respects *Eocramatia* is closest to the Taffiidae, but both the impunctate shell and the structure of the cardinalia militate against including it in that family and, in association with other features, call for the erection of a new monotypic family.

Genus ***EOCRAMATIA*** nov.

NAME. An early brachiopod with a mixture (Gk. κρᾶμα) of morphological features.

DIAGNOSIS. Subquadrate, slightly uniplicate plano-convex shells widest at the hinge-line, with a shallow median sulcus in the pedicle valve corresponding to a low median fold in the obscurely sulcate brachial valve ; ornamentation costellate by branching and intercalation tending to thicken between intersections with concentric lamellae ; ventral interarea high, curved apsacline, pseudodeltidium long, arched, foramen submesothyridid, dorsal interarea planar hypercline, chilidium small arching over the dorsal ends of high, thick, narrowly divergent chilidial plates ; shell impunctate.

Ventral interior with flat semi-oval teeth embedded in thick secondary shell, dental plates absent, ventral muscle field indistinct but apparently not extending much beyond delthyrial cavity ; mantle canal system obscure except for subparallel *vascula media* and terminal branches but possibly associated as a pinnate pattern with low thin ridges radiating from vicinity of delthyrial cavity.

Dorsal interior with flattened, slightly indented ventral ends of chilidial plates filling notothyrial cavity and continuous with slightly convex plate-like socket ridges disposed parallel to hinge-line ; notothyrial platform absent so that cardinalia overhang a shallow posteromedian depression passing anteriorly into low narrow median ridge ; adductor muscle field quadripartite bounded by outwardly curving raised ridges ; dorsal mantle canal pattern preserved only peripherally, possibly pinnate.

TYPE SPECIES. *Eocramatia dissimulata* sp. nov. from the Hope Shales.

Eocramatia dissimulata sp. nov.

(Pl. 21, figs. 9, 12, 14, 15 ; Pl. 22, figs. 1–3, 5, 6 ; Text-fig. 10)

DIAGNOSIS. Subquadrate, uniplicate, plano-convex *Eocramatia* with the pedicle valve 74% as long as wide and 18% as deep as long and ornamented by costellae numbering 5 per mm, 5 mm antero-medially of the ventral umbo ; dorsal adductor scars limited to the posterior half of the valve.

DESCRIPTION. Subquadrate, plano-convex *Eocramatia* with 3 pedicle valves averaging 74% as long as wide (range 68% to 81%) and 18% as deep as long (range 17% to 19%) bearing a shallow median sulcus less than one-third as wide as the hinge-line and a brachial valve nearly three-fifths as long as wide bearing a vague median fold, cardinal margins acute ; costellate ornamentation fine, numbering 5 per mm, 5 mm antero-medially of the umbones of 3 pedicle valves ; apsacline ventral interarea 19% as long as the pedicle valve (average for 4 valves, with a range of 15% to 22%) with the pseudodeltidium extending forward for about one-seventh the length of valve, hypercline dorsal interarea shorter.

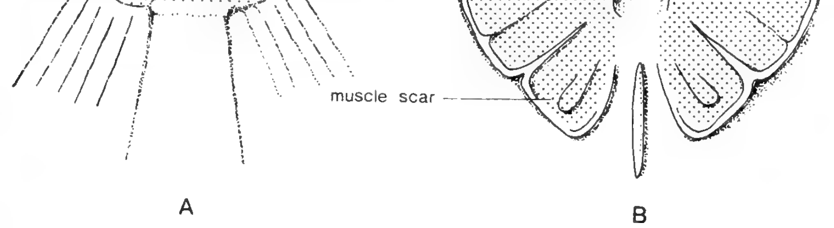


FIG. 10. Diagrammatic views of (A) the ventral interior and (B) the dorsal interior, with a posterior view of the brachial valve above, of *Eocramatia*.

Ventral interior with widely placed teeth extending laterally on either side of the delthyrium for about one-third the width of the pedicle valve, ventral subperipheral rim ill-defined. Dorsal interior with sockets elongated parallel to the hinge-line, dorsal adductor impressions limited to posterior half of the brachial valve.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	External and internal moulds of pedicle valve (BB 35488a, b)	6·8	9·0
PARATYPES	External and internal moulds of brachial valve (BB 35489a, b)	5·2	8·0
	External and internal moulds of pedicle valve (BB 35490a, b)	5·5	7·5
	Incomplete external and internal moulds of conjoined valves (BB 35491a, b)	–	10·5
	External mould of brachial valve (BB 35492)	5·0	–

HORIZON AND LOCALITY. Hope Shales cropping out in Brithdir farmyard, 1 mile ENE of Old Church Stoke (Grid Ref. SO 301953).

DISCUSSION. No other species has yet been described that can profitably be compared with *E. dissimulata*, and as the new species is represented by only a small number of moulds few statistics can be compiled from the sample to indicate the variability of diagnostic features. These are incorporated in the description.

Family **SOWERBYELLIDAE** Öpik 1930

Subfamily **SOWERBYELLINAE** Öpik 1930

SOWERBYELLA Jones 1928

Sowerbyella antiqua Jones emended A. W.

(Pl. 22, figs. 4, 7–14; Pl. 23, figs. 1, 3, 4)

1928 *Sowerbyella antiqua* Jones : 419.

DIAGNOSIS. Semicircular *Sowerbyella* with a brachial valve 51% as long as wide, external surface very rarely ornamented by impersistent rugae finely parvicostellate with a modal count of 10 ribs per mm, 2 mm antero-medially of the dorsal umbo, infrequently segregated into sectors with a mean width of 0·57 mm; ventral muscle scar extending forward for 32% of the length of the pedicle valve; dorsal interior with a median septum usually flanked by 3 pairs of lateral septa, extending anteriorly for 56% of the length of the brachial valve and commonly united into a raised platform at the 4 mm growth stage.

DESCRIPTION. Semicircular *Sowerbyella* with acute cardinal angles, planar or very gently concave brachial valve 51% as long as wide, uniformly convex pedicle valve 27% as deep as long (range 14% to 34% for 11 specimens); ventral and dorsal interareas apsacline and anacline respectively with a supra-apical foramen and a small pseudodeltidium and a complementary chilidium; ornamentation almost exclusively parvicostellate with counts of 9, 10, 11 and 12 ribs per mm, 2 mm antero-medially of the umbones of 6, 30, 19 and 9 brachial valves and differentiated into sectors with a mean width of 0·57 mm, 2 mm antero-medially of the umbo in 24 out of 64 valves ; rugae with a wavelength of 0·15 mm rarely developed sporadically in postero-lateral areas.

Teeth small, dental plates obsolescent ; ventral muscle field strongly cordate in outline, 74% as long as wide and extending forward for 32% of the length of the pedicle valve ; adductor scars small, impressed as two hollows in the secondary shell of the umbo and divided by a fine median ridge ; diductor scars splayed anteriorly and divided by divergent *vascula media* of a lemniscate mantle canal system.

Cardinalia consisting of a median cardinal process fused with chilidial plates and widely divergent socket plates extending anteriorly for 36% of their lateral spread and for 12% of the length of the brachial valve ; notothyrial platform poorly developed ; lophophore and muscle supports consisting of a median septum almost invariably flanked by 3 pairs of lateral septa and extending anteriorly for 56% of the length of the brachial valve, commonly ankylosed to form an elevated cleft platform in adult valves more than 4 mm long.

FIGURED MATERIAL.

	length	width (mm)
External mould of brachial valve (BB 35524)	4·5	9·2
Incomplete internal mould of brachial valve (BB 35525)	–	–
External mould of brachial valve (BB 35526)	5·0	10·0
Internal mould of pedicle valve (BB 35527)	6·0	8·5
External mould of pedicle valve (BB 35528)	6·0	–
Incomplete internal mould of brachial valve (BB 35529)	3·0	–
Internal mould of brachial valve (BB 35530)	3·4	7·0
Incomplete internal mould of brachial valve (BB 35531)	4·6	–
Internal mould of brachial valve (BB 35532)	5·0	10·0
Internal mould of pedicle valve (BB 35533)	5·0	9·0
Incomplete internal mould of pedicle valve (BB 35534)	2·5	–

HORIZON AND LOCALITY. Flags of the Ffairfach Group exposed on the western side of Coed Duon near Llangadog (Grid Ref. SN 709256).

***Sowerbyella* cf. *antiqua* Jones**

(Pl. 23, figs. 2, 5–13)

DIAGNOSIS. Like *Sowerbyella antiqua* but with a ventral muscle scar extending forward for only 26% of the length of the pedicle valve.

DESCRIPTION. Semicircular, concavo-convex *Sowerbyella* with acute cardinal angles, brachial valve 50% as long as wide, pedicle valve 15% as deep as long ; ventral and dorsal interareas apsacline and anacline respectively with a supra-apical foramen and a small pseudodeltidium and complementary chilidium ; ornamentation exclusively parvicostellate with counts of 8, 9, 10, 11 and 12 ribs per mm, 2 mm antero-medially of the umbones of 3, 6, 10, 7 and 1 brachial valves respectively, and segregated into sectors by thickened costellae in only 2 out of 27 valves.

Teeth small, dental plates obsolescent, cordate ventral muscle field 62% as long as wide and extending forward for 26% of the length of the pedicle valve; muscle scars and mantle canal system differentiated as in *S. antiqua* s.s.

Cardinalia consisting of a median cardinal process fused with chilidial plates and widely divergent socket plates extending anteriorly for 10% of the length of the brachial valve and for an average of 28% of their lateral spread in 6 valves (range 25% to 35%); notothyrial platform poorly developed; lophophore and muscle supports consisting of a median septum flanked by 3 pairs of lateral septa, rarely more or fewer, united by secondary shell into a cleft platform in 2 out of 13 specimens over 3·5 mm long.

Figured material.

	length	width (mm)
External mould of brachial valve (BB 35535)	2·5	5·5
Incomplete external mould of brachial valve (BB 35536)	2·3	–
Internal mould of pedicle valve (BB 35537a)	3·0	6·0
External mould of pedicle valve (BB 35537b)	2·8	5·8
Internal mould of brachial valve (BB 35538)	2·5	5·2
Internal mould of pedicle valve (BB 35539)	3·0	5·5
Incomplete internal mould of pedicle valve (BB 35540)	4·3	–
Internal and incomplete external moulds of brachial valve (BB 35541a, b)	4·3	8·0
Incomplete internal mould of brachial valve (BB 35542)	2·5	–

Horizon and locality. Flags transitional from the Meadowtown to Betton Beds exposed in a ploughed field 180 yds south-west of a wall in side of lane from Meadowtown to Castle Ring (Grid Ref. SJ 310009).

Sowerbyella multiseptata sp. nov.

(Pl. 23, figs. 14–19: Pl. 24, figs. 1, 3)

Diagnosis. Semicircular *Sowerbyella* with a brachial valve 51% as long as wide, external surface very rarely ornamented by impersistent rugae, finely parvicostellate with a modal count of 10 ribs per mm, 2 mm antero-medially of the dorsal umbo; ventral muscle scar extending forward for 32% of the length of the pedicle valve; dorsal interior with a late-developing median septum usually flanked by 3 pairs of lateral septa extending anteriorly for 73% of the length of the brachial valve.

Description. Semicircular *Sowerbyella* with acute, rarely orthogonal, cardinal angles; brachial valve 51% as long as wide uniformly gently concave, occasionally with a narrow median fold extending from a protegulum 0·2 mm long to die out anteriorly; pedicle valve convex, rarely subcarinate, with a mean depth of 17% relative to the length of 4 valves (range 16% to 19%); ventral and dorsal interareas apsacline and anacline respectively with a supra-apical foramen and a small pseudodeltidium and complementary chilidium; ornamentation almost exclusively finely parvicostellate with counts of 8, 9, 10 and 11 ribs per mm, 2 mm antero-medially of the umbones of 1, 1, 7 and 4 brachial valves respectively ; impersistent postero-lateral rugae very rare with a wavelength of 0·25 mm.

Teeth small, dental plates obsolescent, cordate ventral muscle field 71% as long as wide and extending forward for 32% of the length of the pedicle valve ; adductor scars small, impressed in 2 hollows in the umbonal secondary shell and divided by a fine median ridge, splayed diductor scars divided by divergent *vascula media.*

Cardinalia consisting of a median cardinal process fused with chilidial plates and widely divergent socket plates extending anteriorly for an average of 30% of their lateral spread and for 10% of the length of 3 brachial valves ; notothyrial platform poorly developed ; lophophore and muscle supports extending anteriorly for 73% of the length of the brachial valve and consisting of a relatively short median septum developing later than a pair of strong submedial septa normally with 2 additional pairs of septa occurring lateral of the median triad, septa becoming united into a cleft platform in 2 out of 10 specimens over 2·5 mm long.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	Internal mould of brachial valve (BB 35544)	2·8	5·3
PARATYPES	External and internal moulds of pedicle valve (BB 35545a, b)	2·6	4·8
	Internal and incomplete external moulds of pedicle valve (BB 35546a, b)	3·0	6·0
	Internal and incomplete external moulds of brachial valve (BB 35547a, b)	3·5	6·5
	External and internal moulds of pedicle valve (BB 35548a, b)	5·3	9·5
	Incomplete internal mould of brachial valve (BB 35549)	1·5	–

HORIZON AND LOCALITIES. Spy Wood Grit : BB 35547 from exposures on top of ridge 1440 yds NNE of Rorrington bench mark 599 (Grid Ref. SJ 303018) ; all other specimens from exposures 1100 yds NNE of Rorrington (Grid Ref. SJ 303015).

***Sowerbyella* cf. *sericea permixta* Williams**

(Pl. 24, figs. 2, 4–7, 10)

1963 *Sowerbyella sericea* (J. de C. Sowerby) *permixta* Williams : 434.

DIAGNOSIS. Semicircular *Sowerbyella* with a brachial valve 50% as long as wide, external postero-lateral surfaces infrequently ornamented by up to 7 pairs of impersistent rugae with a wavelength of 0·3 mm and by fine parvicostellae with modal counts of 10 per mm, 2 mm antero-medially of the dorsal umbo and commonly differentiated into sectors with a mean width of 0·67 mm ; ventral muscle scar extending forward for 42% of the length of the pedicle valve ; dorsal interior with a median septum occurring rarely and developing late, submedial septa strong, usually flanked by a low platform with or without the differentiation of 2 pairs of lateral septa and extending anteriorly for 66% of the length of the brachial valve.

Description. Semicircular *Sowerbyella* with acute cardinal angles becoming roundly obtuse in late growth stages, planar to gently concave brachial valve 50% as long as wide, pedicle valve 19% as deep as long, evenly convex to subcarinate in transverse profile ; ventral and dorsal interareas apsacline and anacline respectively with a supra-apical foramen and a small pseudodeltidium and complementary chilidium ; radial ornamentation normally unequally parvicostellate (in 25 out of 32 brachial valves) with rib counts of 8, 9, 10, 11 and 12 per mm, 2 mm antero-medially of the umbones of 2, 7, 15, 7 and 1 brachial valves respectively, with a mean width of sectors delineated by thickened costellae of 0·67 mm ; up to 7 pairs of rugae with a wavelength of 0·3 mm usually poorly and impersistently developed in the postero-lateral areas at acute angles to the hinge-line.

Teeth small, dental plates obsolescent, cordate ventral muscle field 71% as long as wide and extending anteriorly for 42% of the length of the pedicle valve ; adductor scars small, deeply inserted in a pair of hollows in the umbonal secondary shell and divided by a fine median ridge ; diductor scars splayed anteriorly and divided by *vascula media* forming part of a lemniscate mantle canal system.

Cardinalia consisting of a median cardinal process fused with chilidial plates and widely divergent socket plates extending anteriorly for 33% of their lateral spread and for 13% of the length of the brachial valve ; notothyrial platform poorly developed ; lophophore and muscle supports normally consisting of 3 pairs of septa with a strong submedial pair extending anteriorly for 66% of the length of the brachial valve making up a low cleft platform ; a short median septum was developed in only 3 out of 20 valves less than 4 mm long and in 9 out of 24 valves more than 4 mm long.

Figured material.

	length	width (mm)
External and internal moulds of pedicle valve (BB 35551a, b)	7·0	13·0
External and internal moulds of brachial valve (BB 35552a, b)	3·8	7·5
External and internal moulds of brachial valve (BB 35553a, b)	4·2	8·2
External and internal moulds of brachial valve (BB 35554a, b)	4·7	9·0

Horizon and locality. Aldress Shales exposed in the bank of Ox Wood Dingle at the south-west corner of Ox Wood a few yards north of the Rorrington–Wotherton road (Grid Ref. SJ 290007).

***Sowerbyella* cf. *sericea* (J. de C. Sowerby)**

(Pl. 24, figs. 11, 13, 14, 16)

1839 *Leptaena sericea* J. de C. Sowerby : 636.
1928 *Sowerbyella sericea* (J. de C. Sowerby) Jones : 414.
1963 *Sowerbyella sericea* (J. de C. Sowerby) Williams : 430.

Diagnosis. Semicircular *Sowerbyella* with a brachial valve 50% as long as wide and a pedicle valve 26% as deep as long, ornamented by up to 9 pairs of impersistent rugae with a wavelength of 0·3 mm, and unequally developed parvicostellae with a modal count of 9 per mm, 2 mm antero-medially of the dorsal umbo ; ventral muscle scar extending forward for 30% of the length of the pedicle valve ; dorsal interior with strong submedian septa extending anteriorly for 69% of the length of the brachial valve.

DESCRIPTION. Semicircular *Sowerbyella* with obtusely rounded cardinal angles in adult shells, gently concave brachial valve 50% as long as wide (with a range of 47% to 52% for 5 valves), pedicle valve with a mean depth relative to length of 26% for 6 valves (range 18% to 31%) with steeply sloping sides ; ventral and dorsal interareas apsacline and anacline respectively with a supra-apical foramen and a small pseudodeltidium and complementary chilidium ; radial ornamentation unequally parvicostellate with counts of 7, 8, 9, 10 and 11 ribs per mm, 2 mm antero-medially of the umbones of 1, 2, 4, 3 and 1 brachial valves respectively, with sectors delineated by thickened costellae having a mean width of 0·93 mm (for 8 estimates with a range of 0·7 to 1·2 mm) ; up to 9 pairs of rugae with a modal wavelength of 0·3 mm occur in the postero-lateral areas at acute angles to the hinge-line.

Teeth small, dental plates obsolescent, cordate ventral muscle field 65% as long as wide and extending anteriorly for an average of 30% of the length of 6 pedicle valves (range 24% to 38%) ; adductor scars deeply inserted in a pair of hollows in the umbonal secondary shell and divided by a fine median ridge ; diductor scars splayed anteriorly and divided by *vascula media* forming part of a lemniscate mantle canal system.

Cardinalia consisting of a median cardinal process fused with chilidial plates and widely divergent socket plates extending anteriorly for 35% of their lateral spread and for an average of 14% of the length of 3 brachial valves ; notothyrial platform poorly developed ; lophophore and muscle supports normally consisting of a semicircular platform with strong septa bounding a median cleft extending anteriorly for 69% of the length of brachial valves (range 60% to 75%).

FIGURED MATERIAL.

	length	width (mm)
Internal mould of pedicle valve (BB 35555)	8·7	14·0
External and internal moulds of brachial valve (BB 35556a, b)	6·3	12·0
Pedicle valve (BB 35557)	9·0	13·5

HORIZON AND LOCALITIES. Whittery Shales : BB 35555 from exposures in the lower part of the west bank of the River Camlad, 60 yds north-east of Marrington Farm (Grid Ref. SO 272970) ; BB 35556 from Whittery Quarry at the south end of Whittery Wood, near Chirbury (Grid Ref. SO 275981) ; BB 35557 from exposures in the stream at the north end of Spring Coppice 865 yds south-east of Hockleton Bridge (Grid Ref. SO 279997).

DISCUSSION. Species of *Sowerbyella* found in the Shelve succession belong to two distinct supra-specific groups which may eventually prove to be worth recognizing taxonomically in the manner proposed by Rõõmusoks (1959 : 43), although *S. antiqua* and *S. multiseptata* are not characterized by a differentiated radial ornamentation like that found in the otherwise similar type species of his subgenus *Viruella*. Those taken from the Meadowtown Beds and Spy Wood Grit are characterized by a finely parvicostellate ornamentation only infrequently differentiated into sectors delineated by thickened ribs, and by the rare development of rugae, acutely disposed to the hinge-line, in the postero-lateral areas. The dorsal interiors of mature valves are further distinguished by the almost invariable presence of a median septum flanked by 3 pairs of septa in various stages of coalescence. The occurrence of a median septum in these stratigraphically older *Sowerbyella* is especially significant although the timing of its appearance in relation to the submedial septa was different. In the Meadowtown sample, the median septum is at least as strongly developed as the submedial pair even in the smallest valve (1·5 mm long), which suggests that the septa were secreted more or less simultaneously presumably after the transformation of the trocholophous lophophore into a schizolophe. In the Spy Wood sample, on the other hand, the median septum is shorter than the submedial pair, and in 3 moulds less than 2 mm long it was either absent or weak indicating that it developed later than the submedial septa.

At this juncture it can be stated that the Meadowtown specimens are indistinguishable from a sample of *S. antiqua* Jones from Ffairfach flags of the Llandeilo area, not only in the early development of the median septum but in every other morphological feature except for the greater length of the ventral muscle scar in *S. antiqua* s.s. ($p < 0·001$). Although this difference is statistically significant, it seems reasonable to compare the Meadowtown material with the Welsh species.

The Spy Wood specimens differ significantly from both samples of *S. antiqua* not only in the late development of the median septum but also in the relatively faster anterior spread of the septa ($0·02 > p > 0·01$), and in the slower lateral growth of the brachial valve relative to its increase in length ($0·01 > p > 0·001$). These differences are sufficient to warrant the recognition of a new species, *S. multiseptata*, based on the Spy Wood sample.

The second distinctive group of *Sowerbyella* includes specimens recovered from the younger Aldress Shales and the Whittery and Hagley Shales. Only the Aldress sample is big enough to indicate the range of septa development. It does, however, demonstrate a further significant reduction in the development of a median septum compared with even its relatively late appearance in *S. multiseptata*. Only a pair of strong submedial septa occurred in 4 moulds less than 2·5 mm long; and a short septum had developed in only 3 out of 24 larger valves. No immature specimens of *Sowerbyella* were recovered from the Whittery and Hagley Shales, but traces of a septum were not seen in any of the 4 brachial valves examined which were between 3 and 6·6 mm long.

Comparisons of the Aldress and Whittery samples with described Caradocian *Sowerbyella* indicate that they are closely comparable with *S. sericea* (J. de C. Sowerby). The Aldress specimens in particular could be well tested statistically in relation to recently described species (Williams 1963 : 430–447). It was found that they differed from *S. sericea permixta* Williams only in the relatively wider spread of the ventral muscle scar ($p < 0·001$). The Whittery and Hagley specimens, however, are more like *S. sericea* s.s. in the coarser parvicostellate ribbing, the wavelength, number and more regular occurrence of the postero-lateral rugae, and the greater relative depth of the pedicle valve. Provisionally, therefore, the stratigraphically youngest *Sowerbyella* are referred to *S. sericea* s.s. and the Aldress forms to the subspecies *permixta*.

TABLE 98

Statistics of length (l) and maximum width (w) of n brachial valves of *S. antiqua* Jones from the Ffairfach Group (A), *S.* cf. *antiqua* from the Meadowtown Beds (B), *S. multiseptata* sp. nov. from the Spy Wood Grit (C) and *S.* cf. *sericea permixta* Williams from the Aldress Shales (D)

	A	B	C	D
n	44	31	10	20
$\bar{l}$ mm	3·77	2·66	2·27	3·94
(var l)	(0·851)	(0·508)	(0·333)	(3·096)
$\bar{w}$ mm	7·45	5·36	4·42	7·83
(var w)	(3·039)	(2·112)	(0·971)	(12·016)
r	0·956	0·989	0·987	0·995
$\overline{\log_e l}$	1·2988	0·9427	0·7885	1·2817
(var $\log_e l$)	(0·0579)	(0·0695)	(0·0626)	(0·1815)
$\overline{\log_e w}$	1·9816	1·6437	1·462	1·9685
(var $\log_e w$)	(0·0532)	(0·0708)	(0·0484)	(0·1789)
r_e	0·964	0·995	0·992	0·996
α	0·9582	1·0094	0·8795	0·9928
(var α)	(0·00153)	(0·00036)	(0·00161)	(0·00046)

TABLE 99

Statistics of length (l) and maximum depth (th) of n pedicle valves of *S.* cf. *antiqua* from the Meadowtown Beds (B) and *S.* cf. *sericea permixta* Williams from the Aldress Shales (D) (see Table 98)

	B	D
n	10	9
$\bar{l}$ mm (var l)	3·28 (0·491)	5·11 (3·194)
$\overline{th}$ mm (var th)	0·49 (0·023)	0·97 (0·232)
r	0·883	0·795
a (var a)	0·2175 (0·0013)	0·2698 (0·00381)

TABLE 100

Statistics of length of pedicle valve (l) and length of ventral muscle scar (sc) in n examples of *S. antiqua* Jones from the Ffairfach Group (A), *S.* cf. *antiqua* from the Meadowtown Beds (B), *S. multiseptata* sp. nov. from the Spy Wood Grit (C) and *S.* cf. *sericea permixta* Williams from the Aldress Shales (D)

	A	B	C	D
n	37	20	15	21
$\bar{l}$ mm	4·71	3·24	3·45	5·2
(var l)	(0·831)	(0·869)	(0·941)	(3·101)
$\overline{sc}$ mm	1·5	0·85	1·09	2·2
(var sc)	(0·157)	(0·119)	(0·146)	(1·109)
r	0·885	0·947	0·967	0·953
$\overline{\log_e l}$	1·532	1·1359	1·201	1·5954
(var $\log_e l$)	(0·0367)	(0·0794)	(0·076)	(0·1083)
$\overline{\log_e sc}$	0·3697	−0·239	0·0316	0·6878
(var $\log_e sc$)	(0·0675)	(0·153)	(0·1153)	(0·2055)
r_e	0·898	0·954	0·969	0·9611
α	1·3567	1·3878	1·2317	1·3776
(var α)	(0·01014)	(0·00959)	(0·00712)	(0·00761)

TABLE 101

Statistics of length (l) and width (w) of ventral muscle scar in n pedicle valves of *S. antiqua* Jones from the Ffairfach Group (A), *S.* cf. *antiqua* from the Meadowtown Beds (B), *S. multiseptata* sp. nov. from the Spy Wood Grit (C), and *S.* cf. *sericea permixta* Williams from the Aldress Shales (D)

	A	B	C	D
n	33	15	7	18
$\bar{l}$ mm	1·51	0·83	1·16	2·32
(var l)	(0·154)	(0·081)	(0·209)	(1·054)
$\bar{w}$ mm	2·04	1·33	1·63	3·28
(var w)	(0·216)	(0·167)	(0·339)	(1·581)
r	0·869	0·974	0·975	0·961
$\overline{\log_e l}$	0·3767	−0·2373	0·0734	0·7534
(var $\log_e l$)	(0·0656)	(0·1101)	(0·1451)	(0·1783)
$\overline{\log_e w}$	0·6873	0·2429	0·4276	1·1204
(var $\log_e w$)	(0·0506)	(0·0895)	(0·1202)	(0·1368)
r_e	0·874	0·975	0·977	0·965
α	0·8782	0·9018	0·91	0·8758
(var α)	(0·00585)	(0·00306)	(0·00756)	(0·00325)

TABLE 102

Statistics of length (l) and maximum anterior extension of socket ridges (lc) in n brachial valves of *S. antiqua* Jones from the Ffairfach Group (A), *S.* cf. *antiqua* from the Meadowtown Beds (B) and *S.* cf. *sericea permixta* Williams from the Aldress Shales (D)

	A	B	D
n	40	20	32
$\bar{l}$ mm	4·26	2·97	4·13
(var l)	(0·716)	(0·684)	(1·768)
$\overline{lc}$ mm	0·5	0·28	0·52
(var lc)	(0·016)	(0·012)	(0·041)
r	0·918	0·945	0·918
$\overline{\log_e l}$	1·4305	1·0531	1·3685
(var $\log_e l$)	(0·0386)	(0·0742)	(0·0987)
$\overline{\log_e lc}$	−0·7301	−1·3233	−0·7273
(var $\log_e lc$)	(0·0639)	(0·1363)	(0·1419)
r_e	0·924	0·954	0·924
α	1·2867	1·3554	1·1991
(var α)	(0·00633)	(0·00923)	(0·00704)

TABLE 103

Statistics of maximum anterior (l) and maximum lateral (w) extensions of socket ridges in n brachial valves of *S. antiqua* Jones from the Ffairfach Group (A) and *S.* cf. *sericea permixta* Williams from the Aldress Shales (D)

	A	D
n	28	21
$\bar{l}$ mm (var l)	0·52 (0·056)	0·54 (0·036)
$\bar{w}$ mm (var w)	1·47 (0·107)	1·59 (0·209)
r	0·678	0·826
$\overline{\log_e l}$ (var $\log_e l$)	−0·7365 (0·1844)	−0·6789 (0·1186)
$\overline{\log_e w}$ (var $\log_e w$)	0·3595 (0·0483)	0·4274 (0·0789)
r_e	0·696	0·835
α (var α)	0·5117 (0·00519)	0·8159 (0·0106)

TABLE 104

Statistics of length (l) and maximum anterior extension of septa (ls) in n brachial valves of *S. antiqua* Jones from the Ffairfach Group (A), *S.* cf. *antiqua* from the Meadowtown Beds (B), *S. multiseptata* sp. nov. from the Spy Wood Grit (C) and *S.* cf. *sericea permixta* Williams from the Aldress Shales (D)

	A	B	C	D
n	54	35	13	43
l mm	4·2	2·98	2·73	4·07
(var l)	(0·599)	(0·591)	(0·424)	(1·876)
$\overline{\mathrm{ls}}$ mm	2·34	1·81	1·98	2·68
(var ls)	(0·195)	(0·2)	(0·305)	(0·861)
r	0·926	0·954	0·915	0·969
a	0·5697	0·5817	0·8478	0·6774
(var a)	(0·00088)	(0·00092)	(0·01065)	(0·00068)

Subfamily **AEGIROMENINAE** Havlíček 1961

SERICOIDEA Lindström 1953

Sericoidea cf. ***abdita*** Williams

(Pl. 24, figs. 8, 9, 12, 15, 17, 18 ; Pl. 28, fig. 16)

1955 *Sericoidea abdita* Williams : 418.

DIAGNOSIS. Semicircular *Sericoidea* with a brachial valve 54% as long as wide and ornamented by unequally developed parvicostellae commonly numbering 11 or 12 per mm, 2 mm antero-medially of the dorsal umbo ; median and submedial septa in adult brachial valves extending forwards for about two-thirds the valve length bounded anteriorly by an arc of septules.

DESCRIPTION. Semicircular, concavo-convex *Sericoidea* with a concave brachial valve averaging 54% as long as wide in 6 valves (range 50% to 64%) and an evenly convex pedicle valve with a mean depth for 3 valves of 11·3% (range 8·7% to 13·6%) ; ventral and dorsal interareas apsacline and anacline, supra-apical foramen open in adult pedicle valves ; protegulum about 0·2 mm long ; radial ornamentation unequally parvicostellate with rib frequencies of 11, 12 and 13 per mm, 2 mm antero-medially of the umbones of 3, 3 and 1 brachial valves, divided into sectors about 0·5 mm wide by accentuated costae and costellae ; impersistent rugae with a wavelength of about 0·1 mm occur postero-laterally at acute angles to the hinge-line.

Ventral interior with unsupported oblique teeth ; subquadrate ventral muscle scar about as wide as long and extending forward for 28% of the length of the pedicle valve, bounded by low subparallel ridges trailing anteriorly from the tooth bases and divided postero-medially by a thin median ridge.

Dorsal interior with widely splayed socket ridges extending anteriorly for about 8% of the length of the valve ; lophophore supports of adult valves consisting of a median septum flanked by a pair of submedial septa extending forward for 62·8% of the length of 6 brachial valves (range 54% to 80%) and a peripheral arc of about 8 septules.

FIGURED MATERIAL.

	length	width (mm)
External and incomplete internal moulds of brachial valve (BB 35484a, b)	2·5	3·9
Internal mould of brachial valve (BB 35485)	2·2	4·1
External and internal moulds of brachial valve (BB 35486a, b)	1·3	2·6
External and internal moulds of pedicle valve (BB 35487a, b)	2·2	–

HORIZON AND LOCALITY. Hagley Shales: interbedded tuff exposed in north end of coppice 300 yds north-east of Calcot, Church Stoke (Grid Ref. SO 275961).

DISCUSSION. The only *Sericoidea* found in the Shelve area occur in fine-grained tuffs associated with the Hagley Shales and Volcanics. Specimens are not common but moulds of the brachial valves recovered show that the sample is closely related to *S. abdita* Williams from the Derfel Limestone of the Arenig area (Williams in Williams & Whittington 1955 : 418 ; Williams 1962 : 188). In the smallest brachial valves up to 1·6 mm long the median septum and a peripheral arc of sharp tubercles were strongly developed but the submedial septa only incipiently so. Further growth included an acceleration in the secretion of the submedial septa to amalgamate with the median septum and an accentuation of the arc of tubercles into discrete septules. Both *S. abdita* from Wales and *S.* aff. *abdita* from the Balclatchie Group of Girvan were characterized by the development of a similarly differentiated and proportioned lophophore platform. Indeed the only differences between the Shelve *Sericoidea* and those from Wales and Scotland is that the ribbing of the former is slightly coarser and the brachial valve relatively longer, although on available evidence these differences are not significant.

Superfamily **STROPHOMENACEA** King 1846

Family **STROPHOMENIDAE** King 1846

Subfamily **FURCITELLINAE** Williams 1965

FURCITELLA Cooper 1956

Furcitella sp.

(Pl. 25, figs. 4, 5)

The external and internal moulds of a strophomenid brachial valve (BB 35422a, b), from the Whittery Shales exposed in Whittery Quarry at the south end of Whittery Wood near Chirbury (Grid Ref. SO 275981), have been provisionally identified as *Furcitella*. The valve which was 7·5 mm long was almost semicircular in outline with slightly obtuse cardinal angles. The valve was also resupinate, being flat up to the 2.5 mm growth stage but thereafter becoming convex to attain an overall depth of 10% of the length. The external surface was ornamented by fine, equally developed costellae numbering 8 per mm, 5 mm antero-medially of the umbo and crossed by fine fila with frequencies of up to 18 per mm. The surface also undulated as impersistent rugae with wavelengths of about 0·5 mm. The internal features are poorly preserved but the cardinalia and muscle boundaries can be identified as including a bilobed cardinal process, widely divergent socket ridges, a notothyrial platform extending forward for less than one-third the length of the valve into a median ridge possibly bifurcating anteriorly, and a pair of divergent transmuscle septa.

In respect of its ornamentation, profile and internal features, the brachial valve is not only identifiable as *Furcitella* but also closely comparable with the type species *F. plicata* from the Oranda Formation of Virginia (Cooper 1956 : 877), although on the basis of impressions of only one valve specific identification would not be reliable.

MURINELLA Cooper 1956

Murinella sp.

(Pl. 25, figs. 2, 3)

The incomplete external and internal moulds of a pedicle valve (BB 35421a, b), collected from the Meadowtown Beds exposed along the lane to Lower Ridge from bench mark 754, Little Weston (Grid Ref. SO 293984), are best identified as the strophomenid *Murinella*. The valve was 6·5 mm long and, when complete, must have been semi-elliptical in outline with slightly acute cardinal angles, and evenly convex with only a faintly developed median carina, giving a maximum depth relative to length of about 10%. The ornamentation was finely costellate with 6 ribs per mm at 5 mm antero-medially of the umbo, crossed by fine fila and coarser sporadically occurring growth lines. A pedicle foramen truncated the beak and the relatively small teeth protruding dorsally of the apsacline interarea were supported by short, widely divergent dental plates. The muscle scar was transversely elliptical, extending forward for about one-third the length of the valve and about two-thirds as long as wide. The various components of the muscle field are not identifiable but there is a conspicuous median septum culminating in a point at the anterior boundary of the scar and trailing forward beyond the boundary for a short distance as a low ridge.

The nature of the radial ornamentation, the even convexity of the valve and especially the presence of a median septum in the muscle scar differentiate the valve as belonging to *Murinella*. Indeed except for the greater extension of the median septum beyond the anterior boundary of the muscle scar the valve compares closely with the type species for the genus, *M. partita* from the Bromide Formation of Oklahoma (Cooper 1956 : 848) : however, more material may demonstrate that the Shropshire form is quite distinct.

Subfamily **RAFINESQUININAE** Schuchert 1893

RAFINESQUINA Hall & Clarke 1892

Rafinesquina delicata sp. nov.

(Pl. 25, figs. 6–13)

DIAGNOSIS. Plano- to gently concavo-convex *Rafinesquina* with a pedicle valve 8% as deep as long and a brachial valve 79% as long as wide, radial ornamentation unequally parvicostellate with 7 ribs per mm, 10 mm antero-medially of the dorsal umbo; ventral muscle scar feebly impressed subcircular, as long as wide and extending anteriorly for 28% of the length of the pedicle valve; cardinalia delicately developed, notothyrial platform vestigial except in late growth stages.

DESCRIPTION. Plano- to gently concavo-convex, transversely semi-elliptical *Rafinesquina* with cardinal angles normally orthogonal but also obtuse or acute especially the latter in young shells; pedicle valve evenly convex, 8% as deep as long (range 7% to 10% for 6 valves), brachial valve flat or slightly concave, rarely with a dorsally deflected margin, 79% as long as wide with a strongly convex trilobed protegulum 0·7 mm long; ventral interarea apsacline with a large supra-apical foramen and a small pseudodeltidium, dorsal interarea narrow anacline with a large convex, medially indented chilidium; radial ornamentation unequally parvicostellate, rarely with a thickened median rib, with counts of 6, 7, 8 and 9 ribs per mm, 10 mm antero-medially of the umbones of 10, 13, 3 and 1 brachial valves respectively.

Ellipsoidal teeth obliquely disposed parallel with the widely divergent dental plates reaching anteriorly for 9% of the length of the pedicle valve; ventral muscle field subcircular, 99% as wide as long and extending forward for 28% of the length of the valve, usually faintly developed and consisting of a broad adductor scar impressed on either side of a median ridge and a pair of flanking semicircular diductor scars; internal surface rarely coarsely tuberculate, mantle canal system unknown.

Cardinal process lobes delicate, plate-like, slightly splayed and ankylosed to widely divergent thin socket ridges extending anteriorly for 9% of the length of the brachial valve and 31% of their lateral extension; concave surfaces of narrow sockets normally tuberculate in adult valves; notothyrial platform poorly developed except as a low anchor-shaped feature in late adult growth stages so that the cardinalia usually bound slight postero-medial hollows in younger valves; median ridge and transmuscle septa rarely developed, extending forward for about two-fifths the length of the valve; only the posterior pair of reniform adductor scars known, extending anteriorly for 30% of the length of the valve; subperipheral rim, up to 2 mm wide, rarely developed.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	External and internal moulds of brachial valve (BB 35558a, b)	12·5	17·0
PARATYPES	External and internal moulds of pedicle valve (BB 35559a, b)	13·0	14·5
	External and internal moulds of pedicle valve (BB 35560a, b)	14·0	–
	External and internal moulds of pedicle valve (BB 35561a, b)	11·5	12·0
	Incomplete internal mould of brachial valve (BB 35562)	–	–

	length	width (mm)
External and internal moulds of brachial valve (BB 35563a, b)	10·0	11·5
External and internal moulds of brachial valve (BB 35564a, b)	7·5	9·0

Horizon and localities. Meadowtown Beds: BB 35558 and BB 35564 from exposures 100 yds south-east of Minicop Farm (Grid Ref. SJ 315018); all other specimens from Quinton's Quarry in a field 200 yds north-east of Meadowtown Chapel (Grid Ref. SJ 312013).

Discussion. The *Rafinesquina* found sporadically in the Betton Beds and occurring abundantly in the Meadowtown Beds (Tables 105–110) is especially characterized by the delicacy of its cardinalia, the weakness of its notothyrial platform and the smallness of its subcircular ventral muscle scar. Indeed if it were not for the presence of strongly developed dental plates, the species would have been more appropriately classified as *Platymena* (Cooper 1956 : 879). The nature of these features also serves to distinguish the new species from its closest relative, the Upper Llandeilo *R. simplex* (MacGregor 1961 : 205) which, in particular, has a better defined notothyrial platform and significantly larger ventral muscle scar. In the absence of statistical data from MacGregor's account of *R. simplex*, no other difference may be categorically identified at present, although the brachial valve of the Welsh species may prove to be relatively wider than that of *R. delicata*.

Rafinesquina sp.

(Pl. 25, fig. 1; Pl. 26, fig. 1)

The only specimens from the Whittery Shales referrable to *Rafinesquina* are incomplete complementary external and internal moulds of a brachial valve (BB 35496a, b) recovered from Whittery Quarry at the south end of Whittery Wood, near Chirbury (Grid Ref. SO 275981). The valve was gently concave with a prominent protegulum about 0·5 mm long and an unequally parvicostellate radial ornamentation with a density of 10 ribs per mm antero-medially of the umbo. Impersistent rugae up to 2 mm in wavelength were developed in arcs concentric to the umbo and immediately distinguish the specimen from the Meadowtown *Rafinesquina*. Internally the cardinal process lobes were ridge-like and slightly divergent and capped postero-medially by a strong chilidium. The socket ridges were narrow and low and the anchor-shaped notothyrial platform weakly developed with only one pair of transmuscle septa evident.

A number of strophomenids have been recorded from the Caradocian rocks of England and Wales as *Rafinesquina expansa* (Sowerby) but the species requires revision because, as currently understood (Davidson 1871 : 312), it includes specimens that are not even congeneric; and until more material is available no comparisons are trustworthy.

Table 105

Statistics of length (l) and maximum width (w) of 37 brachial valves of *Rafinesquina delicata* sp. nov.

$\bar{l}$ mm (var l)	6·92 (17·715)
$\bar{w}$ mm (var w)	8·75 (25·535)
r	0·994
$\overline{\log_e l}$ (var $\log_e l$)	1·7778 (0·3143)
$\overline{\log_e w}$ (var $\log_e w$)	2·0247 (0·2880)
r_e	0·996
α (var α)	0·9572 (0·00022)

Table 106

Statistics of length (l) and maximum anterior extension of socket ridges (lc) in 18 brachial valves of *Rafinesquina delicata* sp. nov.

$\bar{l}$ mm (var l)	10·64 (16·557)
$\overline{lc}$ mm (var lc)	0·98 (0·15)
r	0·937
a (var a)	0·095 (0·00006)

Table 107

Statistics of maximum anterior (l) and maximum lateral (w) extensions of socket ridges in 10 brachial valves of *Rafinesquina delicata* sp. nov.

$\bar{l}$ mm (var l)	0·86 (0·198)
$\bar{w}$ mm (var w)	2·61 (0·934)
r	0·928
$\overline{\log_e l}$ (var $\log_e l$)	−0·2694 (0·2374)
$\overline{\log_e w}$ (var $\log_e w$)	0·8951 (0·1283)
r_e	0·937
α (var α)	0·7352 (0·00819)

Table 108

Statistics of length (l) and length of dental plates (dl) in 45 pedicle valves of *Rafinesquina delicata* sp. nov.

$\bar{l}$ mm (var l)	11·16 (16·566)
$\overline{dl}$ mm (var dl)	1·03 (0·124)
r	0·864
a (var a)	0·0867 (0·00004)

Table 109

Statistics of length (l) and length of ventral muscle scar (sc) in 25 pedicle valves of *Rafinesquina delicata* sp. nov.

$\bar{l}$ mm (var l)	12·4 (10·79)
$\overline{sc}$ mm (var sc)	3·51 (1·804)
r	0·916
$\overline{\log_e l}$ (var $\log_e l$)	2·4839 (0·0677)
$\overline{\log_e sc}$ (var $\log_e sc$)	1·1867 (0·1366)
r_e	0·923
α (var α)	1·4209 (0·01296)

TABLE 110

Statistics of length (l) and width (w) of the ventral muscle scar in 23 pedicle valves of *Rafinesquina delicata* sp. nov.

$\bar{l}$ mm (var l)	3·6 (1·351)
$\bar{w}$ mm (var w)	3·56 (1·107)
r	0·96
a (var a)	0·9052 (0·00302)

KJAERINA (HEDSTROEMINA) Bancroft 1929

Kjaerina (Hedstroemina) sp.

(Pl. 26, fig. 2)

The internal mould of a pedicle valve (BB 35452) from the Spy Wood Grit cropping out 1100 yds NNE of Rorrington (Grid Ref. SJ 303015) will probably be shown to represent a new species of the *Kjaerina* species group known as *Hedstroemina* (Bancroft 1929 : 56). The convex valve was about 20 mm long and an estimated 30 mm wide with roundly obtuse cardinal angles affected by a strong but sharply obtuse geniculation to define a relatively flat disc about 10·5 mm long and a trail 15 mm long. Fragments of the external mould at the antero-medial margin indicated that the radial ornamentation was coarsely unequally parvicostellate with about 4 ribs per mm. The ventral interarea was strongly apsacline, the foramen large and supra-apical with a small or resorbed pseudodeltidium. The well-developed teeth were supported by divergent dental plates subtending an angle of about 100° and extending forward for about 15% of the length of the disc. Low convergent ridges extended from the anterior ends of the dental plates to enclose a subcircular muscle field about 70% as long as the disc with a broad median adductor scar extending anteriorly as far as the subflabellate diductor impressions.

The specimen is quite distinct from other known *Hedstroemina* in the strong geniculation of the valve and the large size of the scar in relation to the disc. The Actonian *H. robusta* (Bancroft 1929 : 59) and *H. holtedahli* (Spjeldnaes 1957 : 131) from the 4bα–β horizons of Norway compare most closely, but neither is so sharply deflected nor characterized by so small a disc.

Subfamily **GLYPTOMENINAE** Williams 1965

BYSTROMENA gen. nov.

NAME. A strophomenacean with the posterior of the adult pedicle valve blocked by a plug (Gk. *βύστρα*).

DIAGNOSIS. Concavo-convex, semi-elliptical strophomenids with large protegula, ornamented by parvicostellae which may be unequally developed in early growth stages ; ventral and dorsal interareas apsacline and anacline respectively, pseudodeltidium bounding a large supra-apical foramen truncating the ventral beak, arched chilidium relatively large.

Ventral interior with obliquely placed teeth supported by short widely divergent dental plates ; umbonal region of mature valves occupied by a short cylindroid plug of secondary shell with a median groove on the dorsal surface ; ventral muscle scar obscure, floors of mature valve with many radiating partitions suggesting a lemniscate mantle canal system.

Dorsal interior with delicate cardinalia consisting of a small bilobed cardinal process with a vestigial median ridge present between the lobes in young specimens, each lobe continuous with widely divergent socket ridges ; notothyrial platform absent in young specimens so that the postero-medial part of the valve floor enclosed by the cardinalia forms a hollow which is filled in mature valves by a low median ridge bifurcating anteriorly ; muscle scars obscure with two pairs of transmuscle septa identifiable in young specimens but masked in adult valves by strongly developed radiating partitions associated with a lemniscate mantle canal system.

TYPE SPECIES. *Bystromena perplexa* sp. nov. from the Spy Wood Grit of the Shelve area, Shropshire.

DISCUSSION. The shape of the shell, the disposition of the teeth and their supports and the delicacy of the cardinalia indicate that the new genus is closely related to the Glyptomeninae (Williams in Williams *et al.* 1965 : H388). Yet other features immediately distinguish *Bystromena* from known members of that subfamily. They include the tendency for the ribbing to be costellate rather than unequally parvicostellate, although the general pattern is like that of *Platymena* (Cooper 1956 : 879), and the development of radiating partitions in the interior of adult shells. However, the most important distinction is undoubtedly the cylindroid mass of secondary shell plugging the postero-medial part of the beak interior in adult shells. The plug is in striking contrast to the well-developed foramen in young valves. There are, moreover, indications that the anterior surface of the plug forms a hollow which suggests that the structure was an internal pedicle tube, like those found in some triplesiaceans (Wright 1963 : 744), but filled in with secondary shell following atrophy of the pedicle.

Bystromena perplexa sp. nov.

(Pl. 25, fig. 14 ; Pl. 26, figs. 3–14 ; Pl. 27, figs. 1, 2 ; Text-fig. 11)

DIAGNOSIS. Transversely semi-elliptical *Bystromena* with a brachial valve about three-quarters as long as wide and gently concave umbonally flattening peripherally in maturity, and an evenly convex pedicle valve about one-tenth as deep as long ; radial ornamentation finely costellate in adult shells with a modal count of 7 per mm, 5 mm antero-medially of the umbo.

DESCRIPTION. Transversely semi-elliptical *Bystromena* with slightly acute to obtuse cardinal angles, brachial valve about three-quarters as long as wide, slightly concave in the umbonal region but flattening peripherally in adult growth stages, pedicle valve evenly convex and about one-tenth as deep as long, protegulum large, trilobed up to 1 mm long ; radial ornamentation commonly unequally parvicostellate in early growth stages but becoming costellate in adult shells with counts of 5, 6, 7

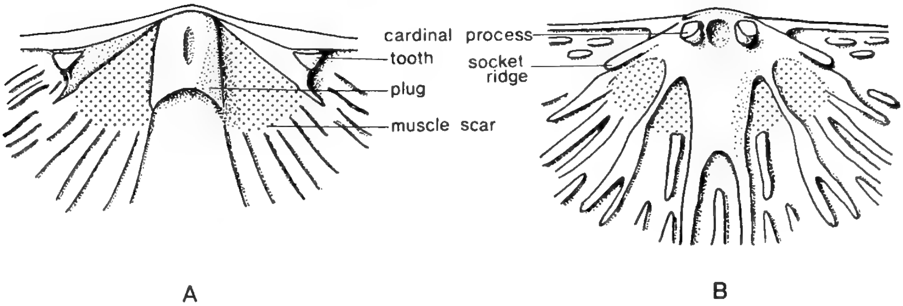


FIG. 11. Diagrammatic views of (A) the ventral and (B) the dorsal interiors of *Bystromena*.

and 8 ribs per mm, 5 mm antero-medially of the umbones, of 3, 1, 4 and 1 valves respectively ; ventral and dorsal interareas apsacline and anacline respectively with a functional foramen at least in young pedicle valves, and well-developed pseudodeltidium and chilidium.

Teeth obliquely disposed ridges supported by widely divergent dental plates extending anteriorly for less than one-tenth of the pedicle valve ; ventral muscle field obscure, cylindroid infilled pedicle tube, with a shallow median furrow on the dorsal surface, extending anteriorly for about 1 mm ; floor of mature valve ornamented by many radiating thin partitions.

Cardinal process small with vestigial median ridge present between the lobes in immature valves, lobes continuous with widely divergent socket ridges subtending an angle of about 135° ; notothyrial platform absent except in mature valves when it extended forward for a short distance as a median ridge bifurcating anteriorly ; transmuscle septa present but usually obscured by radiating thin partitions delineating a pinnate mantle canal system ; dorsal muscle impressions obscure.

TYPE MATERIAL.

		length	width (mm)
HOLOTYPE	Internal mould of pedicle valve (BB 35363)	8·0	11·5
PARATYPES	External and internal moulds of incomplete pedicle valve (BB 35364a, b)	–	–
	External and internal moulds of pedicle valve (BB 35365a, b)	6·0	8·0
	External and internal moulds of pedicle valve (BB 35366a, b)	4·5	–
	External and internal moulds of brachial valve (BB 35367a, b)	5·0	6·5
	External and internal moulds of brachial valve (BB 35368a, b)	4·0	–
	Incomplete internal mould of pedicle valve (BB 35369)	–	–
	Incomplete internal mould of brachial valve (BB 35370)	–	–

Type horizon and localities. Spy Wood Grit: BB 35363, 35365 from exposures on top of ridge 1440 yds NNE of Rorrington bench mark 599 (Grid Ref. SJ 303018); BB 35364, 35370 from outcrops 1100 yds NNE of Rorrington (Grid Ref. SJ 303015); BB 35368, 35369 from the north bank of Spy Wood Brook, 170 yds north-east of Spy Wood Cottage (Grid Ref. SO 282958); BB 35366, 35367 from exposures 700 yds NNW of Middleton Church (Grid Ref. SO 296998).

Discussion. As far as is known, no previously described species can be assigned to *Bystromena*; and even *B. perplexa* is represented by only a few moulds, mostly imperfectly preserved, from the Spy Wood Grit so that much remains to be discovered about the variability of the new species itself.

Family **LEPTAENIDAE** Hall & Clarke 1894

LEPTAENA Dalman 1828

Leptaena cf. ***ventricosa*** Williams

(Pl. 27, figs. 5, 8, 9)

Diagnosis. *Leptaena* with a semicircular disc about 10 mm long, ornamented by relatively coarse costellae numbering 4 per mm, 5 mm antero-medially of the umbo and about 9 low concentric rugae on the disc with a wavelength of 1 mm, subcircular ventral muscle scar less than two-thirds as long as the disc.

Description. Concavo-convex, sharply geniculate and subquadrate *Leptaena* with a semicircular disc about 10 mm long, almost twice as wide and about one-eighth as deep in the vicinity of the ventral umbo, well defined by a confining fold with a wavelength of 2 mm, trail sharply deflected at about 90° to give an overall depth of about half the length of the pedicle valve; ventral and dorsal interareas apsacline and anacline respectively with a small pseudodeltidium truncated by a large open supra-apical foramen and a well-developed chilidium; radial ornamentation finely but evenly costellate with 4 per mm, 5 mm antero-medially of the umbo; 9 more or less continuous concentric rugae with a wavelength of about 1 mm also ornament the disc.

Teeth obliquely disposed and supported by short widely divergent dental plates; ventral muscle field not well preserved but apparently rhomboidal in outline and about three-fifths as long as the disc.

Cardinalia poorly preserved but a strong bilobed cardinal process, widely splayed socket ridges and an anchor-shaped notothyrial platform were identifiable, as were the transmuscle septa especially the longer, curved submedial pair which extend anteriorly for about four-fifths of the length.

Figured material.

	length	width (mm)
External and internal moulds of brachial valve (BB 35453a, b)	–	–
Internal mould of pedicle valve (BB 35454)	–	–

Horizon and localities. Whittery Shales: BB 35454 from exposures in the stream at the north end of Spring Coppice, 865 yds south-east of Hockleton Bridge

(Grid Ref. SO 279997) ; BB 35453 from exposures half-way down the path going southwards below Marrington Farm (Grid Ref. SO 272967).

Discussion. The few impressions of *Leptaena* found in the Whittery and Hagley Shales compare very closely with those of *L. ventricosa* Williams (1963 : 462) from the Gelli-grin Group of the Bala district. The disc of *L. ventricosa* s.s., which is about three-fifths as long as wide, as well as the ventral muscle scar, may prove to be consistently longer ; but provisionally the Shropshire material is reasonably identified as conspecific with the Welsh.

KIAEROMENA Spjeldnaes 1957

Kiaeromena cf. ***kjerulfi*** (Holtedahl)

(Pl. 27, figs. 6, 10, 11)

1916 *Leptaena kjerulfi* Holtedahl : 72.
1957 *Kiaeromena kjerulfi* (Holtedahl) Spjeldnaes : 183.
1963 *Kiaeromena* cf. *kjerulfi* (Holtedahl) Williams : 464.

Diagnosis. Obtusely geniculate *Kiaeromena* with a disc about 12 mm long, ornamented by up to 9 coarse concentric rugae and unequally developed parvicostellae numbering about 6 per mm, 10 mm antero-medially of the ventral umbo ; subcircular ventral muscle field about 6 mm long.

Description. Subquadrate *Kiaeromena* with a rounded obtuse angle of geniculation to define a plano-convex disc about 12 mm long and almost twice as wide ornamented by up to 9 coarse concentric asymmetric rugae with wavelengths of 1·5 mm and steeper posterior slopes ; radial ornamentation unequally parvicostellate especially on the trail with a count of 6 per mm, 10 mm antero-medially of the ventral umbo ; ventral and shorter dorsal interareas apsacline and anacline respectively with the pseudodeltidium and beak pierced by a large supra-apical foramen, and an arched chilidium.

Ventral interior with trigonal teeth supported by divergent dental plates acting as the posterior boundaries of a poorly preserved subcircular muscle scar extending forward for about 6 mm.

Dorsal interior with a cardinal process consisting of a small median ridge flanked by two acutely divergent lobes and poorly defined socket ridges supported by a massive, anchor-shaped notothyrial platform.

Figured material.

	length	width (mm)
Incomplete external and internal moulds of pedicle valve (BB 35406a, b)	25	–
Incomplete external and internal moulds of brachial valve (BB 37132a, b)	–	–

Horizons and localities. BB 35406 from Whittery Shales exposed in the lower part of the west bank of the River Camlad, 60 yds north-east of Marrington Farm (Grid Ref. SO 272970) ; BB 37132 from Hagley Volcanics exposed in a roadside quarry 150 yds north of Church Stoke Hall (Grid Ref. SO 274942).

Discussion. Only a few incomplete moulds of a finely ribbed, obtusely geniculate leptaenid have been recovered from the Hagley and Whittery Shales. There is no doubt, however, about the generic identity of the specimens which compare sufficiently closely with *Kiaeromena* cf. *kjerulfi*, occurring rarely in the Allt Ddu Group of the Bala district (Williams 1963 : 464), to be regarded as conspecific.

Order PENTAMERIDA Schuchert & Cooper 1931
Suborder SYNTROPHIIDINA Ulrich & Cooper 1936
Superfamily **PORAMBONITACEA** Davidson 1853
Family **SYNTROPHIIDAE** Schuchert 1896
Subfamily **XENELASMATINAE** Ulrich & Cooper 1936
EUORTHISINA Havlíček 1950

The genus *Euorthisina* Havlíček (1950 : 16) was not included by Biernat in her review of the Porambonitacea (in Williams *et al.* 1965 : H523–536). But, as demonstrated by Havlíček, the genus is undoubtedly a porambonitacean although unique in its shape within the superfamily. This difference is related to the strong development of wide interareas in both valves and the absence of a dorsal fold and ventral sulcus. Such features are normally quite variable in other articulates but they are so exceptional among the porambonitaceans as to prompt Biernat (1965 : H524) to report that within the superfamily the interareas are 'commonly reduced and scarcely visible' and that the 'anterior commissure is invariably uniplicate'. Neither diagnosis is true of *Euorthisina* which is, accordingly, immediately distinguishable from all other porambonitaceans. Through the kindness of Dr Havlíček, it is possible to figure here internal moulds of *Euorthisina moesta* (Barrande) from the Llanvirnian Šárka formation of Rokycany (Pl. 28, figs. 4, 6, 7) which show the main features of the genus (BB 37160–37162).

Havlíček (1950 : 16) compared his genus with *Xenelasma* (Ulrich & Cooper 1936 : 631) which is also characterized by discrete dental plates and a septalium. It is, however, possible that the internal similarity is an expression of convergence, but until more is known about the ancestry of *Euorthisina* it seems more practicable to follow Havlíček's lead and provisionally retain the genus within the Xenelasmatinae.

Euorthisina cf. ***moesta minor*** Havlíček

(Pl. 28, figs. 1–3, 5, 8)

1950 *Euorthisina moesta minor* Havlíček : 87.

Diagnosis. Subequally and evenly biconvex, transversely suboval *Euorthisina* ornamented by fine lamellae and costellae numbering 3 per mm, 5 mm anteromedially of the ventral umbo ; parallel dental plates and septalium extending forward for about one-fifth the length of their respective valves.

Description. Transversely suboval *Euorthisina* with a gently convex brachial valve about 60% as long as wide and a pedicle valve about 15% as deep as long with an evenly and gently convex transverse profile ; ornamented by fine closely spaced lamellae and rounded ribs composed of 9 primary costae and intercalated costae within 1 mm of the umbo and costellae appearing in later stages of growth by branching and intercalation with counts of 3 ribs per mm, 5 mm antero-medially of the umbones of 2 pedicle valves ; ventral interarea short, almost orthocline, with a narrow open delthyrium ; brachial interarea not exposed.

Ventral interior with simple node-like teeth supported by long parallel dental plates extending forward for an average of one-fifth the length of 3 pedicle valves to define a narrow delthyrial chamber ; muscle and mantle canal impressions unknown.

Dorsal interarea with small septalium supported by a median ridge extending forward for about one-fifth the length of the brachial valve ; muscle and mantle canal impressions unknown.

Figured material.

	length	width (mm)
External and internal moulds of orthocone containing impressions of 4 *Euorthisina* (BB 35377a, b)	–	–
Incomplete external and internal moulds of pedicle valve (BB 35378a, b)	4·5	–
External and internal moulds of pedicle valve (BB 35379a, b)	3·2	–
Incomplete external and internal moulds of brachial valve (BB 35380a, b)	4·5	7·5

Horizon and localities. Mytton Flags : BB 35377, 35378 from the adit in Maddox's Coppice, 1200 yds ENE of St Luke's Church, Snailbeach (Grid Ref. SJ 382030) ; BB 35379, 35380 from outcrops by the side of the cart-track 140 yds north of Wood House, Gravels (Grid Ref. SJ 338003).

Discussion. The small number of moulds of *Euorthisina* collected from the Mytton Flags include a group of 4 poorly preserved conjoined shells all orientated in the same way within an orthocone and probably buried in position of growth. The sample compares most closely with *E. moesta minor* Havlíček from the Llanvirnian Šárka Shales of Czechoslovakia, especially in the relative dimensions and size of the dental plates (cf. Pl. 28, figs. 4, 6, 7). Havlíček (1950 : 87) reports that in his subspecies there are 8 to 12 ribs in the umbonal region compared with 14 to 16 in the Shelve specimens. But this difference may be an expression of variability in the older stock and its systematic importance can only be satisfactorily assessed when more material is available.

Family **PARASTROPHINIDAE** Ulrich & Cooper 1938

PARASTROPHINELLA Schuchert & Cooper 1931

Parastrophinella musculosa sp. nov.

(Pl. 28, figs. 9–13, 17)

Diagnosis. Small, subtriangular, strongly biconvex *Parastrophinella* with vestigial fold and sulcus and commonly 11 to 13 costae, with a wavelength of 0·6 mm, ornamenting the anterior part of the shell.

Description. Small, biconvex, subtriangular *Parastrophinella* with a brachial valve averaging 93% as wide as long and 29% as deep as long (for 4 and 3 valves respectively) and a mean depth of 23% relative to the length of 3 pedicle valves, transverse profile evenly convex with steep lateral slopes, longitudinal profile evenly convex to anteriorly geniculate, dorsal fold and ventral sulcus faintly and sporadically developed ; rostrate with depressed palintropes extending antero-laterally for up to 35% of the maximum width of the shell, delthyrium and notothyrium open ; shell smooth for an average of 3·7 mm anterior of the umbones of 3 specimens, delayed costation consisting of rounded costae with a mean wavelength of 0·56 mm between 5 and 6 mm anterior of the umbones of 7 brachial valves and numbering 10 to 14 in 1, 2, 1, 2 and 1 brachial valves respectively between 5 and 7 mm long.

Ventral interior with small teeth and well-developed spondylium sessile posteriorly but supported anteriorly by a median septum extending forward for an average of 45% of the length of 3 pedicle valves.

Dorsal interior with subparallel outer plates separated by less than one-tenth the maximum width of the brachial valve and extending forward for a mean proportion of 40% of the length of 4 valves ; elongately oval adductor scars impressed on either side of the outer plates for an average of 56% of the length of 3 valves.

Type material.

		length	width (mm)
Holotype	External and internal moulds of pedicle valve (BB 35598a, b)	7·0	8·5
Paratypes	External and internal moulds of brachial valve (BB 35599a, b)	6·0	5·8
	Internal mould of brachial valve (BB 35600)	5·0	5·2
	Internal mould of pedicle valve (BB 37107)	5·5	5·0
	Internal mould of brachial valve (BB 37108)	7·5	7·0

Type horizon and locality. Spy Wood Grit exposed 1100 yds NNE of Rorrington (Grid Ref. SJ 303015).

Discussion. The Spy Wood Grit porambonitacean is an early species of *Parastrophinella* which is like the Upper Llandeilo *P. costata* MacGregor (1961 : 199) except for its significantly fewer, coarser ribs, its relatively greater length and the vestigial nature of its fold and sulcus. These differences are important enough to merit systematic recognition.

***Parastrophinella* sp.**

(Pl. 28, figs. 14, 15)

Incomplete external and internal moulds (BB 35461a, b) of a pedicle valve, collected from the Hagley Volcanics in the roadside quarry 150 yds. north of Church Stoke Hall (Grid Ref. SO 274942), probably represent *Parastrophinella*. The valve, which was 13·5 mm long, was 85% as long as wide and 25% as deep as wide with a persistent flat-bottomed sulcus about 60% as wide as long and evenly convex flanks. Radial ornamentation consisted of rounded costae about 0·8 mm in wavelength, 5 mm antero-medially of the umbo where they arose, and numbered 4 in the sulcus and 8 on each flank. The apsacline interarea was relatively short and curved, and the open delthyrium was flanked by small teeth supported by the walls of a sessile spondylium extending anteriorly for 37% of the length of the valve.

In the absence of a complementary brachial valve, the identification of the remains of the pedicle valve as *Parastrophinella* is provisional. Furthermore, the valve is quite different from older *Parastrophinella* found in Shropshire and Wales with their weak sulci and smooth umbonal regions. More material is, therefore, required not only to indicate the specific affinities of the stock but also to verify the generic status of the specimen.

Order RHYNCHONELLIDA Kuhn 1949

Superfamily **RHYNCHONELLACEA** Gray 1849

Family **TRIGONIRHYNCHIIDAE** McLaren 1965

ROSTRICELLULA Ulrich & Cooper 1942

Rostricellula sparsa Williams

(Pl. 27, figs. 3, 4, 7)

1963 *Rostricellula sparsa* Williams : 467.

Diagnosis. Small, relatively wide *Rostricellula* with 2 costae, averaging 0·4 mm thick 2 mm anterior of the umbo, on a well-developed fold two-fifths as wide as the length of the brachial valve, and 4 to 6 costae on each of the lateral slopes.

Description. Small, biconvex, subtriangular *Rostricellula* with a brachial valve slightly less long than wide (96% for 2 valves) and 15% as deep as long, and a pedicle valve slightly less than one-quarter as deep as long, dorsal fold (and ventral sulcus) strongly developed up to 40% as wide as the length of the brachial valve and rounded in transverse profile with evenly convex lateral slopes ; rostrate with high curved ventral umbo and inconscpicuous dorsal umbo, apical angle about 100°, nature of deltidial plates unknown ; radial ornamentation exclusively costate with 2 rounded costae on the fold, averaging 0·4 mm in wavelength, 2 mm anterior of the umbones of 4 brachial valves, and 4 to 6 on the lateral slopes.

Ventral interior with small teeth supported by slightly divergent dental plates extending anteriorly for about one-eighth the length of the valve ; muscle field unknown.

Hinge-plate of dorsal interior small, divided by septalium extending forward for an average of 8% the length of 4 brachial valves, median ridge low, rounded but developed for about two-fifths the length of the valve ; details of crura and muscle scar unknown.

Figured material.

	length	width (mm)
External and internal moulds of brachial valve (BB 35584a, b)	3·5	3·5
External and internal moulds of pedicle valve (BB 35585a, b)	3·0	–

HORIZON AND LOCALITY. Spy Wood Grit exposed 1100 yds NNE of Rorrington (Grid Ref. SJ 303015).

DISCUSSION. *Rostricellula* is rare in the Shelve area, being represented only by a few valves from the Spy Wood Grit which are quite different in ornamentation and outline from all other described species except *R. sparsa* from the Allt Ddu Mudstones of the Bala district. In every morphological aspect the Spy Wood specimens are identical with the small sample on which the Welsh species was based. Especially significant for immediate identification is the presence of 2 costae on the fold. Only one American and one European species are known with so few ribs. They are: *R.* ? *minuta* from the Hermitage Formation of Tennessee which, although similar in shape, has 7 or 8 costae on each lateral slope (Cooper 1956 : 640); and *R. ambigena* (Barrande) from the Upper Ordovician of Bohemia (Havlíček 1961 : 51) which is not only relatively longer but has the costae on the fold and sulcus branching within the size range of the British species.

Order SPIRIFERIDA Waagen 1883

Suborder ATRYPIDINA Moore 1952

Superfamily **ATRYPACEA** Gill 1871

Family **ATRYPIDAE** Gill 1871

Subfamily **ZYGOSPIRINAE** Waagen 1883

ZYGOSPIRA Hall 1862

Zygospira sp.

(Pl. 27, figs. 12, 13)

An internal mould (BB 37133) has been recovered from Spy Wood Grit outcrops 1100 yds NNE of Rorrington (Grid Ref. SJ 303015), which is likely to represent the remains of a brachial valve of the atrypacean *Zygospira*. The rostrate valve, which was about 2 mm long, was nearly circular in outline and about 15% as deep with a shallow narrow median sulcus and evenly convex lateral areas. The external surface was ornamented by about 15 fine costae while internally a median ridge corresponding to the narrow sulcus supported a divided hinge plate with rounded crural bases.

This occurrence is one of the earliest records of *Zygospira*, which has hitherto been described from younger Ordovician strata in N. America (Cooper 1956 : 672–674), Scotland (Williams 1962 : 242) and Mid-Europe (Havlíček & Vaněk 1966 : 61). The relatively few ribs may be diagnostic but may also reflect immaturity of the specimen and detailed comparison with established species would not be profitable at present.

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VII. REFERENCES

ALICHOVA, T. N. 1953. A guide to the brachiopod fauna in the Ordovician sediments of the north-western part of the Russian Platform. *Trudy vses. nauchno-issled. geol. Inst.*, Leningrad, **1953** : 1–127, pls. 1–17. [In Russian.]

ANDREEVA, O. N. 1960. *Novye vidy drevnikh rasteniy i Bezprovochnykh S.S.S.R.* [Markowskii, B. P., editor-in-chief], **1** : 288 pp., 73 pls. Moscow.

BANCROFT, B. B. 1928. The Harknessellinae. *Mem. Proc. Manchr lit. phil. Soc.*, **72** : 173–196, pls. 1–2.

—— 1929. Some new genera and species of Strophomenacea from the Upper Ordovician of Shropshire. *Mem. Proc. Manchr lit. phil. Soc.*, **73** : 33–65, pls. 1–2.

—— 1945. The brachiopod zonal indices of the stages Costonian to Onnian in Britain. *J. Paleont.*, Menasha, **19** : 181–252, pls. 22–38.

BARRANDE, J. 1848. *Über die Brachiopoden der Silurischen Schichten von Boehmen*, **2** : 153–256, pls. 15–23. Vienna.

—— 1879. *Système Silurien du centre de la Bohême*, **5**. *Classe des Mollusques. Ordre des Brachiopodes.* 226 pp., 153 pls. Prague.

BASSETT, D. A., WHITTINGTON, H. B. & WILLIAMS, A. 1966. The stratigraphy of the Bala district, Merionethshire. *Q. Jl geol. Soc. Lond.*, **122** : 219–271.

BATES, D. E. B. 1968. The Lower Palaeozoic brachiopod and trilobite faunas of Anglesey. *Bull. Br. Mus. nat. Hist.* (Geol.), London, **16** : 127–199, pls. 1–14.

—— 1969. Some early Arenig brachiopods and trilobites from Wales. *Bull. Br. Mus. nat. Hist.* (Geol.), London, **18** : 1–28, pls. 1–9.

COCKERELL, T. D. A. 1911. The name *Glossina*. *Nautilus, Philad.*, **25** : 96.

COOPER, G. A. 1956. Chazyan and related brachiopods. *Smithson. misc. Collns*, Washington, **127** : 1–1024, 1025–1245, pls. 1–269.

DAVIDSON, T. 1868. British Fossil Brachiopoda, **3**. Devonian and Silurian Brachiopoda. *Palaeontogr. Soc.* (*Monogr.*), London, 397 pp., 50 pls.

—— 1883. Supplement to the Fossil Brachiopoda. *Palaeontogr. Soc.* (*Monogr.*), London, 242 pp., 17 pls.

DEAN, W. T. 1958. The faunal succession in the Caradoc Series of south Shropshire. *Bull. Br. Mus. nat. Hist.* (Geol.), London, **3** : 191–231, pls. 24–26.

GORYANSKY, V. 1969. *Inarticulate Brachiopods of the Cambro-Ordovician rock of the north-west Russian Platform.* 126 pp., 21 pls. NEDRA, Leningrad. [In Russian.]

HAVLÍČEK, V. 1949. Orthoidea and Clitambonoidea of the Bohemian Tremadoc. *Sb. st. geol. Ust. čsl. Repub.*, Praha, **16** : 93–144, pls. 1–5.

—— 1950. The Ordovician Brachiopoda from Bohemia. *Rozpr. ústred. Ust. geol.*, Praha, **13** : 1–135, pls. 1–13.

—— 1961. Rhynchonelloidea des Böhmischen Älteren Paläozoikums (Brachiopoda). *Rozpr. ústred. Ust. geol.*, Praha, **27** : 1–211, pls. 1–27.

—— 1967. Brachiopoda of the suborder Strophomenidina in Czechoslovakia. *Rozpr. ústred. Ust. geol.*, Praha, **33** : 1–235, pls. 1–52.

—— 1968. New brachiopods in the Lower Caradoc of Bohemia. *Věst. ústred. Ust. geol.*, Praha, **43** : 123–125, pls. 1–2.

—— 1970. Heterorthidae (Brachiopoda) in the Mediterranean Province. *Sb. geol. Věd. Praha*, (P) **12** : 7–39, pls. 1–11.

—— 1971. Brachiopodes de l'Ordovicien du Maroc. *Notes Mém. Serv. Mines Carte géol. Maroc*, Rabat, **230** : 1–135, pls. 1–26.

—— & VANĚK, J. 1966. The biostratigraphy of the Ordovician of Bohemia. *Sb. geol. Věd. Praha*, (P) **8** : 7–69, pls. 1–16.

HOLTEDAHL, O. 1916. The Strophomenidae of the Kristiania Region. *Skr. VidenskSelsk. Christiania*, **12** : 1–117, pls. 1–16.

JONES, O. T. 1928. *Plectambonites* and some allied genera. *Mem. geol. Surv. Gr. Br. Palaeont.*, London, **1** (5) : 367–527, pls. 21–25.

KOZLOWSKI, R. 1929. Les brachiopodes gothlandiens de la Podolie Polonaise. *Palaeont. pol.*, Warsaw, **1** : 1–254, pls. 1–12.

LAPWORTH, C. & WATTS, W. W. 1894. The geology of South Shropshire. *Proc. Geol. Ass.*, London, **13** : 297–355, pls. 8–9.

MACGREGOR, A. R. 1961. Upper Llandeilo brachiopods from the Berwyn Hills, North Wales. *Palaeontology*, London, **4** : 177–209, pls. 19–23.

MICKWITZ, A. 1909. Vorläufige Mitteilung über das Genus *Pseudolingula* Mickwitz. *Mém. Acad. Sci. St. Petersb.* (6) **3** : 765–772.

MURCHISON, R. I. 1839. *The Silurian System* [&c.]. 768 pp., 37 pls. London.

—— 1859. *Siluria.* 3rd ed. 592 pp., 42 pls. London.

NEUMAN, R. B. 1964. Fossils in Ordovician tuffs, Northeastern Maine. *Bull. U.S. geol. Surv.*, Washington, **1181**-E : 1–38, pls. 1–7.

—— 1968. Paleogeographic implications of Ordovician shelly fossils in the Magog belt of the Northern Appalachian Region. *In* Zen, E-an, *et al.* (eds). *Studies of Appalachian Geology : Northern and Maritime* : 35–48, pls. New York.

NIKIFOROVA, O. I. & ANDREEVA, O. N. 1961. Ordovician and Silurian stratigraphy of the Siberian Platform and its palaeontological basis (Brachiopoda). *Trudy̆ vses. nauchno-issled. geol. Inst.*, Leningrad, **56** : 1–412, pls. 1–56. [In Russian.]

ÖPIK, A. 1930. Brachiopoda Protremata der Estländischen Ordovizischen Kukruse-Stufe. *Tartu Ulik. Geol.-Inst. Toim.*, **20** : 1–261, pls. 1–22.

—— 1934. Über Klitamboniten. *Tartu Ulik. Geol.-Inst. Toim.*, **39** : 1–239, pls. 1–48.

—— 1939. Brachiopoden und Ostrakoden aus dem Expansusschiefer Norwegens. *Norsk geol. Tidsskr.*, Oslo, **19** : 117–142, pls. 1–6.

PHILLIPS, J. 1848. The Malvern Hills, compared with the Palaeozoic districts of Abberley, Woolhope, May Hill, Tortworth and Usk. *Mem. geol. Surv. U.K.*, London, **2** : 1–330, pls. 1–3.

RÕÕMUSOKS, A. K. 1959. Strophomenoidea Ordovika i Silura Estonii 1. Rod *Sowerbyella* Jones. *Tartu Univ. (Dorpat), Act. Commentationes* **75** : 11–41, pls. 1–8.

—— 1970. *Stratigraphy of the Viruan Series (Middle Ordovician) in Northern Estonia.* Tallin, U.S.S.R. 345 pp., 8 pls. [In Russian.]

ROWELL, A. J. 1966. Revision of some Cambrian and Ordovician inarticulate brachiopods. *Paleont. Contr. Univ. Kans.*, Topeka, **7** : 1–36, pls. 1–4.

RUBEL, M. P. 1961. Lower Ordovician brachiopods of the superfamilies Orthacea, Dalmanellacea and Syntrophiacea of the eastern Baltic. *Eesti NSV Tead. Akad. geol. Inst. Uurimused*, **6** : 141–226, pls. 1–27. [In Russian.]

RUDWICK, M. J. S. 1965. Sensory spines in the Jurassic brachiopod *Acanthothiris*. *Palaeontology*, London, **8** : 604–617, pls. 84–87.

SALTER, J. W. 1859. Appendix A. *In* Murchison, R. I. *Siluria*, 3rd ed. : 531–552. London.

—— 1866. Appendix. On the fossils of North Wales. *In* Ramsey, A. C. The Geology of North Wales. *Mem. geol. Surv. U.K.*, London, **3** : 239–381, pls. 1–26.

SCHUCHERT, C. & COOPER, G. A. 1932. Brachiopod genera of the suborders Orthoidea and Pentameroidea. *Mem. Peabody Mus. Yale*, New Haven, **4** : 1–270, pls. 1–29.

SINCLAIR, G. W. 1945. Some Ordovician Lingulid Brachiopods. *Trans. R. Soc. Can.*, Ottawa, (3, iv) **39** : 55–82, pls. 1–4.

SOWERBY, J. DE C. 1839. *In* Murchison, R. I. *The Silurian System* [&c.] : 608–644, pls. 5–22. London.

SPJELDNAES, N. 1957. The Middle Ordovician of the Oslo Region, Norway. 8. Brachiopods of the Suborder Strophomenida. *Norsk geol. Tidsskr.*, Bergen, **37** : 1–214, pls. 1–14.

TEMPLE, J. T. 1968. The Lower Llandovery (Silurian) brachiopods from Keisley, Westmorland. *Palaeontogr. Soc.* (*Monogr.*), London, 58 pp., 10 pls.

—— 1970. The Lower Llandovery brachiopods and trilobites from Ffridd Mathrafal, near Meifod, Montgomeryshire. *Palaeontogr. Soc.* (*Monogr.*), London, 76 pp., 19 pls.

ULRICH E. O. & COOPER, G. A. 1936. New genera and species of Ozarkian and Canadian brachiopods. *J. Paleont.*, Tulsa, **10** : 616–631.

—— —— 1938. Ozarkian and Canadian Brachiopoda. *Spec. Pap. geol. Soc. Am.*, Baltimore, **13** : 1–323, pls. 1–58.

WATTS, W. W. 1925. The geology of South Shropshire. *Proc. Geol. Ass.*, London, **36** : 321–363.

WHITTARD, W. F. 1952. A geology of South Shropshire. *Proc. Geol. Ass.*, London, **63** : 143–197.

—— 1966. The trilobites of the Henllan Ash (Lower Ordovician), Merionethshire. *Bull. Br. Mus. nat. Hist.* (Geol.), London, **11** : 489–505, pls. 1–5.

WHITTINGTON, H. B. & WILLIAMS, A. 1955. The fauna of the Derfel Limestone of the Arenig District, North Wales. *Phil. Trans. R. Soc.*, London, (B) **238** : 397–430, pls. 38–40.

WILLIAMS, A. 1949. New Lower Ordovician brachiopods from the Llandeilo–Llangadock District. *Geol. Mag.*, London, **86** : 161–174, 226–238, pls. 8, 11.

—— 1953. The geology of the Llandeilo district, Carmarthenshire. *Q. Jl geol. Soc. Lond.*, **108** : 177–208.

—— 1962. The stratigraphy and brachiopod faunas of the Barr and Lower Ardmillan Series (Caradoc) of the Girvan district, south-west Ayrshire, with descriptions of the Brachiopoda. *Mem. geol. Soc. Lond.*, **3** : 1–267, pls. 1–25.

—— 1963. The Caradocian brachiopod faunas of the Bala District, Merionethshire. *Bull. Br. Mus. nat. Hist.* (Geol.), London, **8** : 327–471, pls. 1–16.

—— 1973. Distribution of brachiopod assemblages in relation to Ordovician palaeogeography. *In* Hughes, N. F. (ed.). Organisms and Continents through Time. *Spec. Pap. Palaeont.*, London, **12** : 241–269.

—— *et al.* 1965. Brachiopoda. *In* Moore, R. C. (ed.). *Treatise on Invertebrate Paleontology*, **H.** 927 pp., illustr. Kansas.

—— *et al.* 1972. A correlation of Ordovician rocks in the British Isles. *Spec. Rep. geol. Soc. Lond.*, **3** : 1–74, text-figs.

WILSON, A. E. 1913. A new brachiopod from the base of the Utica. *Bull. Victoria meml Mus.*, Ottawa, **1** : 81–84, pl. 8.

WRIGHT, A. D. 1963. The fauna of the Portrane Limestone. I. The inarticulate brachiopods. *Bull. Br. Mus. nat. Hist.* (Geol.), London, **8** : 221–254, pls. 1–4.

—— 1964. The fauna of the Portrane Limestone, II. *Bull. Br. Mus. nat. Hist.* (Geol.), London, **9** : 157–256, pls. 1–11.

—— 1971. Taxonomic significance of the pseudodeltidium in triplesiacean brachiopods. *Palaeontology*, London, **14** : 342–356, pls. 62–63.

INDEX

New taxonomic names and the page numbers of the principal references are printed in **bold** type. An asterisk (*) denotes a figure.

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PLATE 1

Obolus subditivus sp. nov. (p. 25)

Hope Shales, near Brithdir Farm, Shropshire.

FIGS. 1, 3, 2. Holotype, BB 35573a, b. Latex casts of the exterior and interior and the internal mould of a pedicle valve, ×5·6.

FIGS. 5, 6. Paratype, BB 35574a, b. Latex cast of the exterior and the internal mould of a pedicle valve, ×6·3, ×5·8.

FIGS. 4, 8, 7. Paratype, BB 35575a, b. Latex casts of the exterior and interior and the internal mould of a brachial valve, ×5·5.

Obolus sp. (p. 26)

Mytton Flags, Bergam Quarry, Shropshire.

FIG. 9. BB 35581a. Exfoliated pedicle valve, ×4·3.

Mytton Flags, near Wood House, Shropshire.

FIG. 10. BB 35582. Exfoliated brachial valve, ×4·5.

Schmidtites* ? *simplex sp. nov. (p. 26)

Rorrington Beds, Holywell Brook, Shropshire.

FIG. 11. Holotype, BB 37134a. Internal mould of a pedicle valve, ×8.
FIG. 14. Paratype, BB 37138. Internal mould of a brachial valve, ×6·7.

Rorrington Beds, Deadman's Dingle, Shropshire.

FIG. 12. Paratype, BB 37139. Internal mould of a pedicle valve, ×8.

Rorrington Beds, near the Mount, Shropshire.

FIG. 13. Paratype, BB 37136. Exterior of a pedicle valve, ×9.

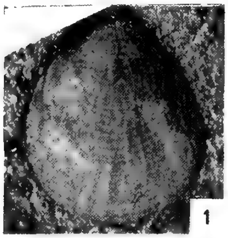
Rorrington Beds, near Desert, Shropshire.

FIG. 15. Paratype, BB 37140a. Internal mould of a pedicle valve, ×8·3.

Schmidtites* ? *simplex subcircularis sp. et subsp. nov. (p. 27)

Stapeley Shales, Whitsburn Dingle, Shropshire.

FIG. 16. Holotype, BB 37141. Exterior of a pedicle valve, ×9·2.
FIG. 17. Paratype, BB 37142b. Latex cast of the external mould of a pedicle valve, ×8.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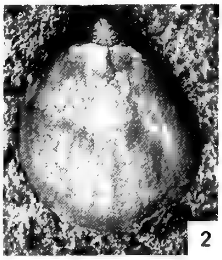
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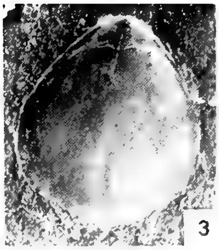
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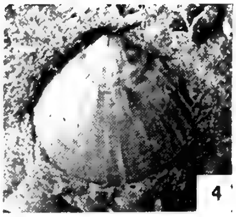
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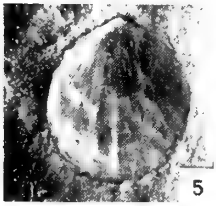
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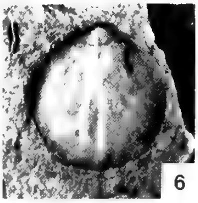
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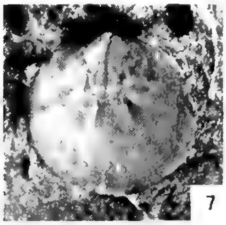
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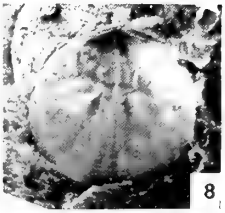
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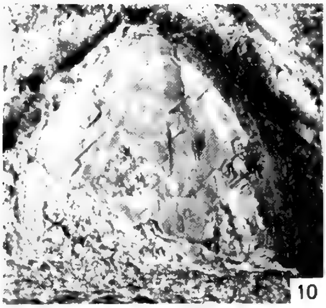
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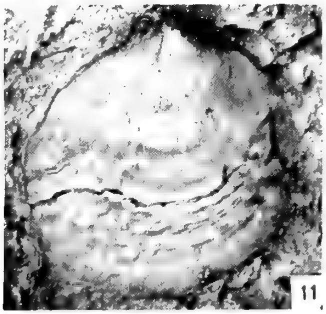
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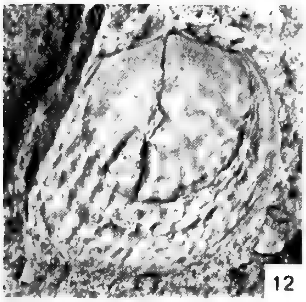
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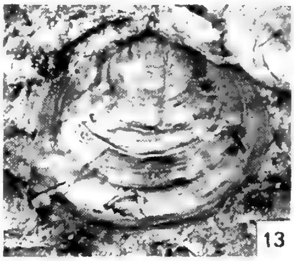
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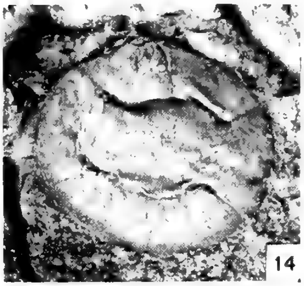
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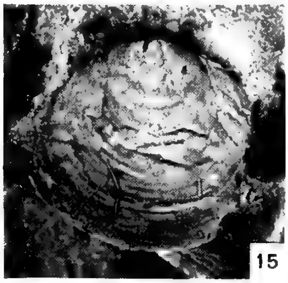
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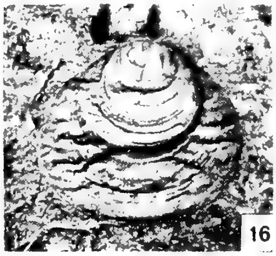
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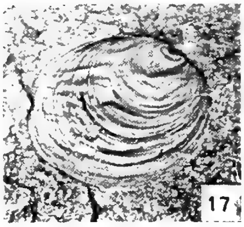
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PLATE 2

Schmidtites ? simplex subcircularis sp. et subsp. nov. (p. 27)

Stapeley Shales, Whitsburn Dingle, Shropshire.

FIG. 1. Paratype, BB 37143a. Internal mould of a brachial valve, ×6.

Lingulella displosa sp. nov. (p. 28)

Meadowtown Beds, Waitchley, Shropshire.

FIG. 2. Paratype, BB 37146a. Internal mould of a pedicle valve, ×3·8.

Meadowtown Beds, near Meadowtown Quarry, Shropshire.

FIGS. 4, 3, 8. Holotype, BB 37144a, b. Latex cast, with detail, of the external mould, and the internal mould of a pedicle valve, ×4, ×12, ×3.

Rorrington Beds, Lower Wood Brook, Shropshire.

FIG. 5. Paratype, BB 37149. Internal mould of a brachial valve, ×2·8.

Meadowtown Beds, Little Weston, Shropshire.

FIG. 6. Paratype, BB 37148a. Internal mould of a pedicle valve, ×3·1.

Meadowtown Beds, near Meadowtown Quarry, Shropshire.

FIG. 7. Paratype, BB 37147a. Internal mould of a brachial valve, ×3.

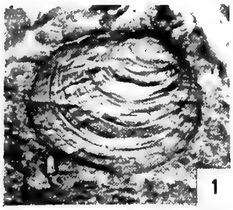
Lingulella displosa petila sp. et subsp. nov. (p. 29)

Stapeley Volcanic Group, Whitsburn Dingle, Shropshire.

FIG. 9. Paratype, BB 37152a. Internal mould of a pedicle valve, ×4.

FIG. 10. Paratype, BB 37151a. Internal mould of a brachial valve, ×4.

FIG. 11. Holotype, BB 37150b. Latex cast of the external mould of a pedicle valve, ×9.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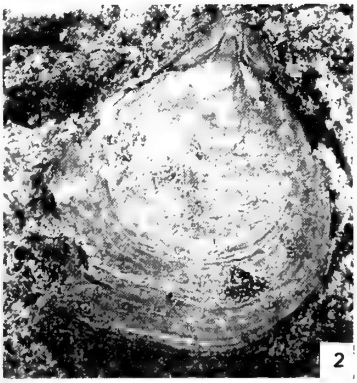
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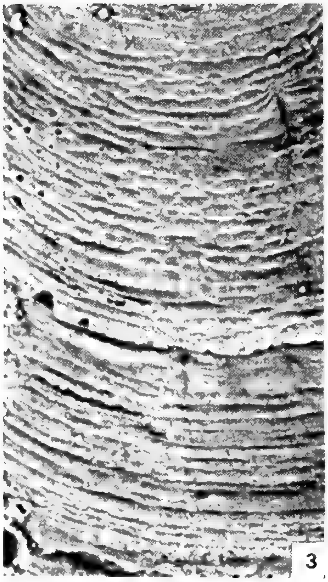
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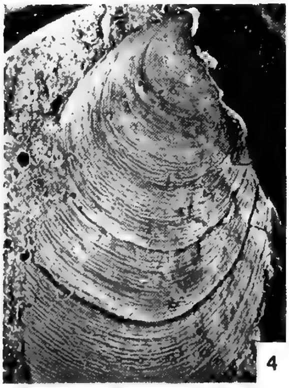
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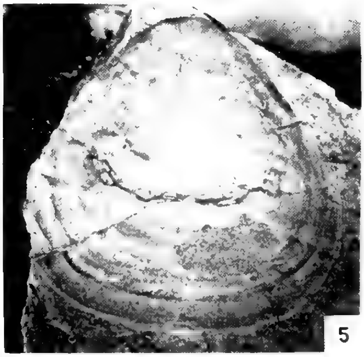
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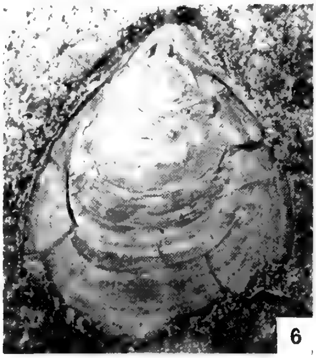
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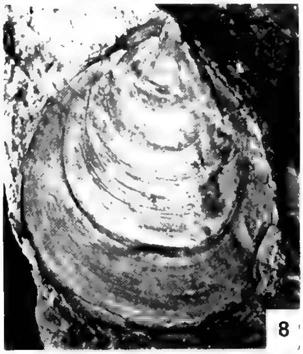
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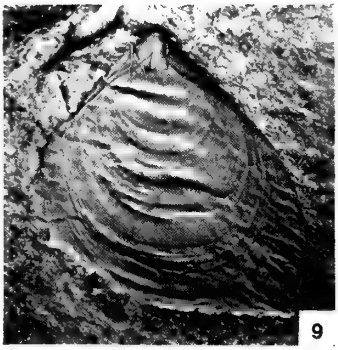
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PLATE 3

Lingulella displosa petila sp. et subsp. nov. (p. 29)

Stapeley Volcanic Group, Whitsburn Dingle, Shropshire.

FIG. 1. Holotype, BB 37150a. Internal mould of a pedicle valve, × 4·5.

Palaeoglossa attenuata (J. de C. Sowerby) (p. 32)

Meadowtown Beds, Lower Wood Brook, Shropshire.

FIG. 2. BB 37109a. Internal mould of a brachial valve, × 3·4.

Meadowtown Beds, Little Weston, Shropshire.

FIG. 3. BB 37110a. Internal mould of a pedicle valve, × 5.

Betton Beds, near junction of Holywell and Whitehouse Brooks, Shropshire.

FIGS. 4, 11. BB 37117a, b. Internal moulds of pedicle and brachial valves, × 6·5, × 6·9.
FIG. 12. BB 37116a. Internal mould of a pedicle valve, × 4·7.

Meadowtown Beds, near Meadowtown Quarry, Shropshire.

FIGS. 7, 5. BB 37113. Exterior, with detail, of a pedicle valve, × 6·5, × 13.
FIG. 8. BB 37115. Internal mould of a pedicle valve, × 2·8.

Meadowtown Beds, near Meadowtown Chapel, Shropshire.

FIG. 6. BB 37111a. Internal mould of a ventral pseudointerarea, × 17·3.
FIG. 9. BB 37112. Latex cast of the exterior of a pedicle valve, × 4·6.
FIG. 10. BB 37114a. Internal mould of a brachial valve, × 5·4.

Rorrington Beds, in stream near Meadowtown Chapel, Shropshire.

FIG. 13. BB 37118b. Internal mould of a brachial valve, × 3·5.


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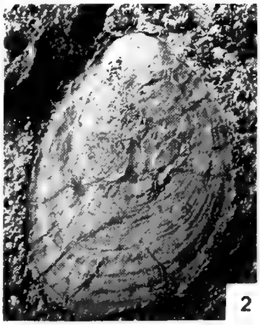
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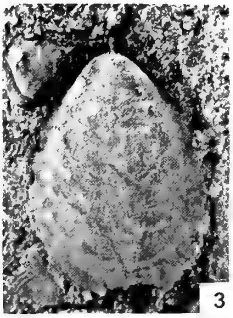
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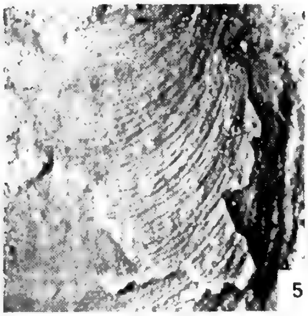
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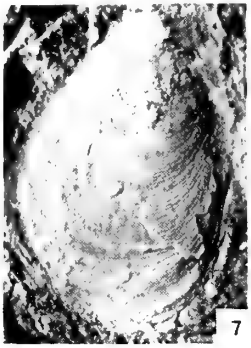
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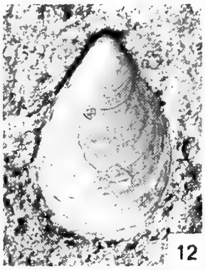
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PLATE 4

Palaeoglossa myttonensis sp. nov. (p. 33)

Mytton Flags, Whitegrit School, Shropshire.

FIGS. 2, 1. Paratype, BB 37122a, b. External and internal moulds of disarticulated valves, × 4·9, × 5·8.

FIG. 4. Holotype, BB 37119. Internal mould of a pedicle valve and an external mould of the complementary brachial valve, × 4·9.

Mytton Flags, near Blakemoorflat, Shropshire.

FIG. 3. Paratype, BB 37123. Internal mould of a brachial valve, × 5·2.

Mytton Flags, New Perkin's Level, Shropshire.

FIG. 5. Paratype, BB 37121a. Internal mould of a brachial valve, × 6.

Pseudolingula spatula sp. nov. (p. 36)

Weston Beds, near Lyde, Shropshire.

FIG. 6. Paratype, BB 37126. Internal mould of a pedicle valve, × 2·9.

FIGS. 7, 10. Paratype, BB 37128a, b. Latex cast of the exterior and the internal mould of a brachial valve, × 3, × 3·2.

FIG. 9. Paratype, BB 37125a. Internal mould of a brachial valve, × 3.

Weston Beds, Cwm Dingle, Shropshire.

FIG. 8. Holotype, BB 37124a. Internal mould of a brachial valve, × 3.

Rorrington Beds, Deadman's Dingle, Shropshire.

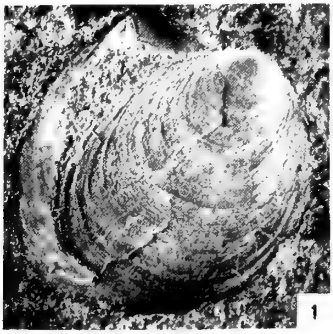
FIG. 11. BB 37130a. Internal mould of a pedicle valve, × 5·5.

Meadowtown Beds, Minicop Farm, Shropshire.

FIGS. 12, 13. BB 37129. Fragments of the external lateral area and the interior of a pedicle valve, × 6, × 6·4.

Mytton Flags, River Camlad, Shropshire.

FIG. 14. BB 35583. Exfoliated pedicle valve, × 3.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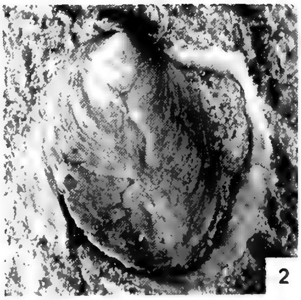
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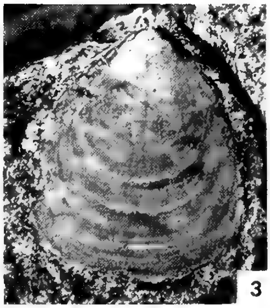
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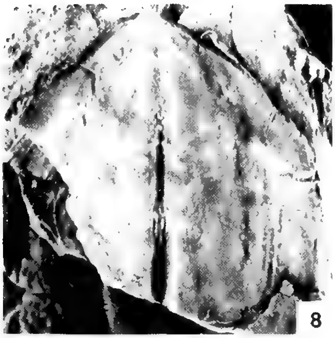
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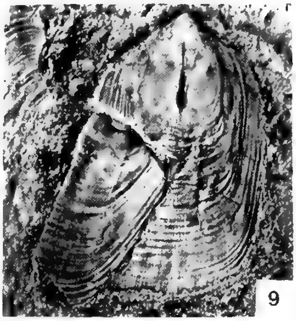
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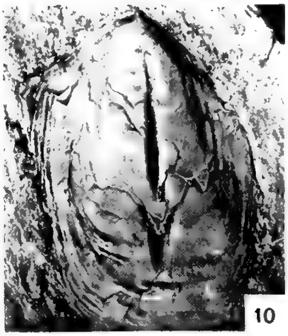
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PLATE 5

Pseudolingula spatula sp. nov. (p. 36)

Weston Beds, near Lyde, Shropshire.

FIG. 1. Paratype, BB 37128b. Detail of the latex cast of the external mould of a brachial valve, ×21.

Monobolina plumbea (Salter) (p. 38)

Mytton Flags, Old Perkin's Level, Shropshire.

FIG. 2. BB 35467. Latex cast of the interior of a pedicle valve, ×3·4.

Mytton Flags, near Snailbeach Coppice, Shropshire.

FIGS. 3, 10. BB 35470a, b. Latex cast of the exterior and the internal mould of a brachial valve, ×5·4, ×3·6.

Mytton Flags, New Perkin's Level, Shropshire.

FIGS. 4, 7. BB 35468. Latex cast, with detail, of the exterior of a pedicle valve, ×6, ×12.

Mytton Flags, Perkin's Beach, Shropshire.

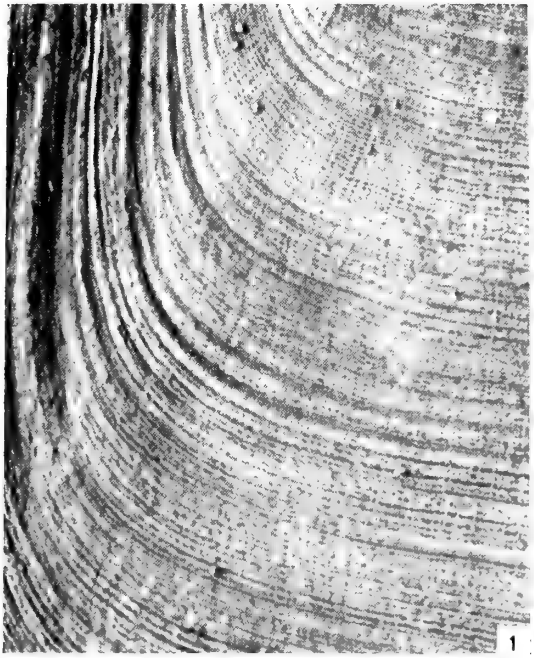
FIGS. 5, 6. BB 35473a. Latex cast of the interior and the internal mould of a pedicle valve, ×2·6.

Mytton Flags, near St Luke's Church, Shropshire.

FIG. 8. BB 35472. Internal mould of a pedicle valve, ×2·4.

Mytton Flags, Mytton Batch, Shropshire.

FIG. 9. BB 35469a. Internal mould of a brachial valve, ×2·8.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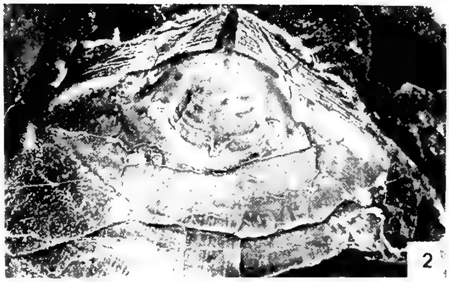
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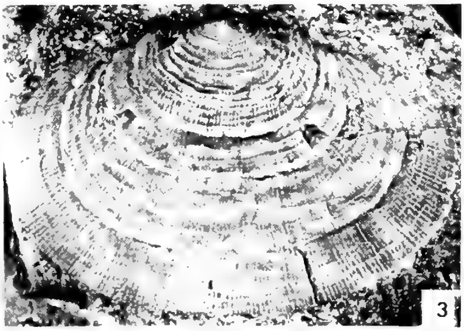
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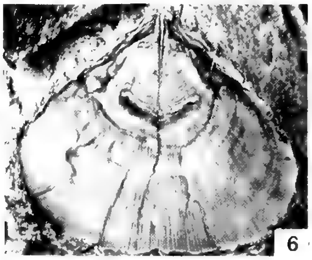
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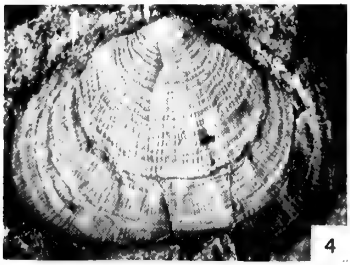
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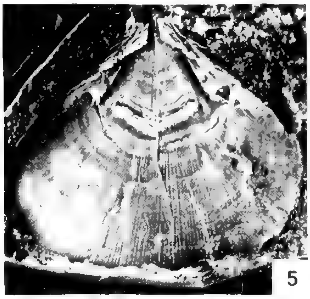
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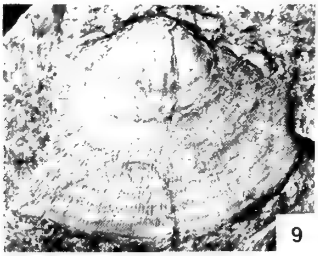
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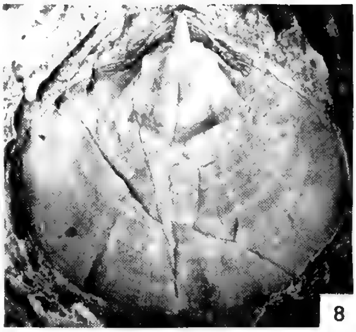
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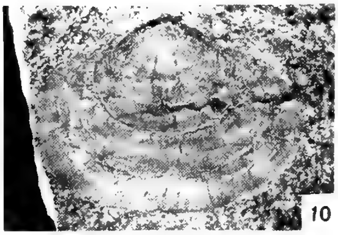
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PLATE 6

Monobolina plumbea (Salter) (p. 38)

Mytton Flags, near Blakemoorflat, Shropshire.

FIG. 1. BB 35471. Latex cast of the internal mould of a pedicle valve, ×2·6.

Paterula cf. ***bohemica*** Barrande (p. 40)

Hope Shales, Hope Dingle, Shropshire.

FIGS. 2, 3. BB 35588a, b. Latex cast of the exterior and the internal mould of a pedicle valve, ×11.

FIGS. 5, 4. BB 35589a, b. Latex cast of the exterior and the internal mould of a brachial valve, ×11·9.

Meadowtown Beds, Minicop Farm, Shropshire.

FIG. 6. BB 35590. Exterior of a pedicle valve, ×6.
FIG. 7. BB 35591. Exterior of a brachial valve, ×11·1.
FIG. 8. BB 35592. Exterior of a pedicle valve, ×11·9.
FIG. 9. BB 35593. Exterior of a pedicle valve, ×11·9.
FIG. 10. BB 35594. Exterior of a brachial valve, ×12·1.
FIG. 11. BB 35595. Exterior of a brachial valve, ×10.

Paterula cf. ***perfecta*** Cooper (p. 41)

Spy Wood Grit, Spy Wood Dingle, Shropshire.

FIG. 12. BB 35597. Exterior of a brachial valve, ×11.
FIG. 13. BB 35596. Exterior of a pedicle valve, ×11·5.

Apsotreta sp. (p. 42)

Mytton Flags, near Wood House, Shropshire.

FIGS. 14, 15. BB 35565a. Ventral and lateral views of the internal mould of a pedicle valve, ×7, ×5.

Conotreta stapeleyensis sp. nov. (p. 43)

Stapeley Shales, Leigh Hall, Shropshire.

FIG. 16. Holotype, BB 35566. Internal mould of a pedicle valve, ×7.

FIG. 17. Paratype, BB 35568. Internal mould of a brachial valve, ×5·7.

FIGS. 18, 19. Paratype, BB 35569. Latex cast of the interior and the internal mould of a brachial valve, ×7, ×6.

FIG. 20. Paratype, BB 35570. Internal mould of a brachial valve with adherent shell posteriorly, ×6.

FIG. 21. Paratype, BB 35571b. Latex cast of the exterior of a pedicle valve, ×5·7.

Schizocrania salopiensis sp. nov. (p. 44)

Rorrington Beds, near Desert, Shropshire.

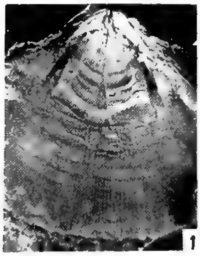
FIG. 22. Paratype, BB 35361. Exterior of a brachial valve, ×7·1.
FIG. 23. Paratype, BB 35362a. Internal mould of a brachial valve, ×4.

Spy Wood Grit, near Rorrington, Shropshire.

FIG. 24. Paratype, BB 35359. Exterior of a brachial valve, ×3·5.
FIG. 25. Holotype, BB 35358a. Internal mould of a brachial valve, ×2·2.

Betton Beds, near Little Weston, Shropshire.

FIG. 26. Paratype, BB 35404a. Internal mould of a brachial valve, ×7.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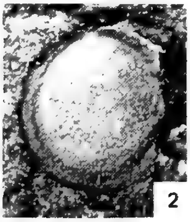
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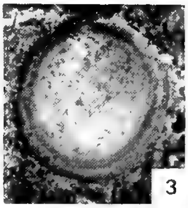
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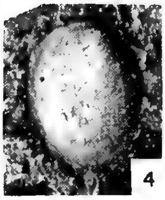
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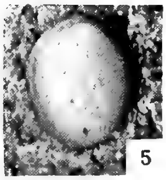
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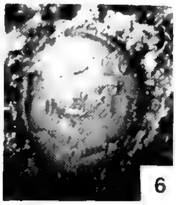
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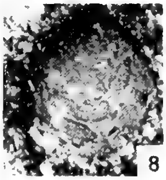
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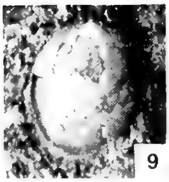
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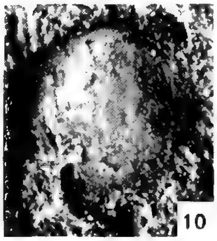
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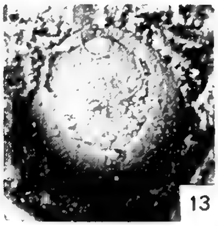
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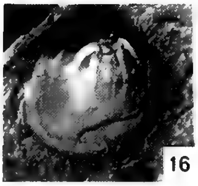
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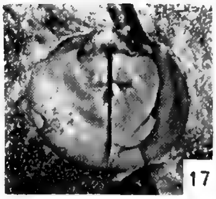
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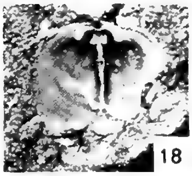
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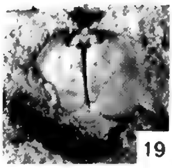
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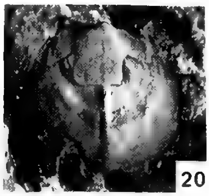
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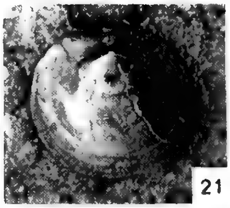
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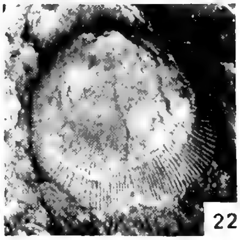
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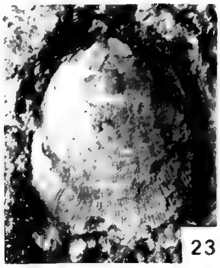
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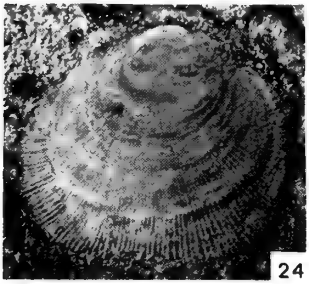
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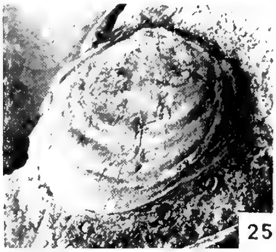
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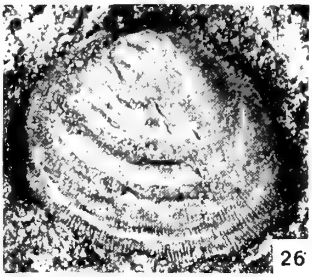
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PLATE 7

Orbiculoidea sp. (p. 47)

Stapeley Shales, Shropshire (unlocated exposure).

FIG. 1. BB 35576. Latex cast of the exterior of a brachial valve, × 5.

Schizotreta transversa sp. nov. (p. 47)

Meadowtown Beds, near Meadowtown Quarry, Shropshire.

FIG. 2. Paratype, BB 35578. Exfoliated pedicle valve, × 6·2.
FIG. 7. Holotype, BB 35577. Exfoliated pedicle valve, × 6·7.

Meadowtown Beds, Middleton, Shropshire.

FIG. 3. Paratype, BB 35579. Exfoliated brachial valve, × 7·1.

Schizotreta sp. (p. 48)

Mytton Flags, New Perkin's Level, Shropshire.

FIG. 4. BB 35580. Latex cast of the exterior of a pedicle valve, × 8.

Petrocrania dubia sp. nov. (p. 48)

Whittery Shales, near Hockleton Bridge, Shropshire.

FIGS. 8, 6, 5. Holotype, BB 35405a, b. Latex casts of the exterior and interior and the internal mould of a brachial valve, × 2·6, × 3·5, × 3.

Hesperonomia sp. (p. 49)

Mytton Flags, Woodside House, Shropshire.

FIGS. 12, 9. BB 35334a, b. Latex casts of the external and internal moulds of a brachial valve, × 8·3, × 5.

Orthis cf. ***callactis*** Dalman (p. 50)

Mytton Flags, Crowsnest Dingle, Shropshire.

FIGS. 10, 11. BB 35498a, b. Latex cast of the exterior and the internal mould of a pedicle valve, × 3·6.

Mytton Flags, near St Luke's Church, Shropshire.

FIG. 13. BB 35500. Latex cast of the exterior of a brachial valve, × 8·4.

FIGS. 15, 14. BB 35497. Latex casts showing dorsal and ventral views of conjoined valves, × 3·4.

FIG. 16. BB 35499. View of a fragment of the internal mould of a brachial valve and the external mould of the complementary pedicle valve, × 12·5.


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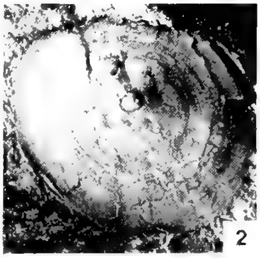
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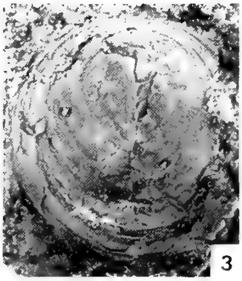
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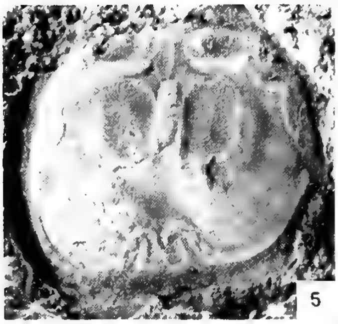
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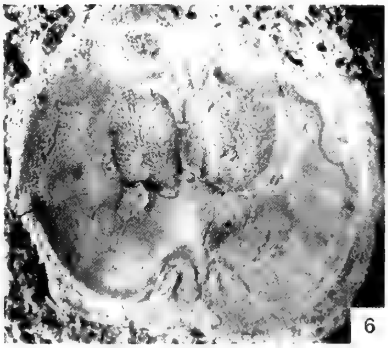
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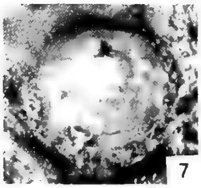
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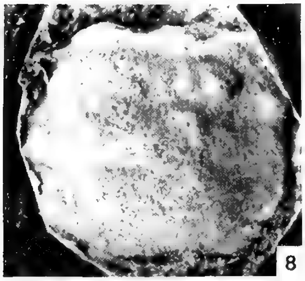
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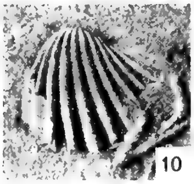
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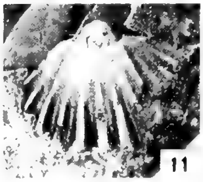
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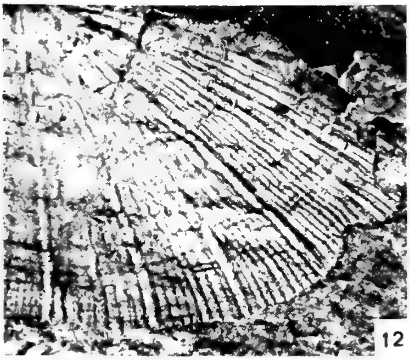
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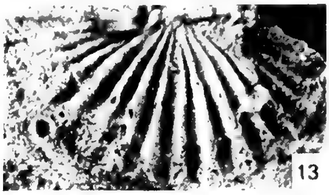
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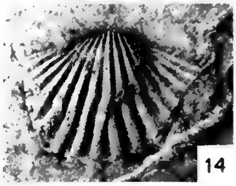
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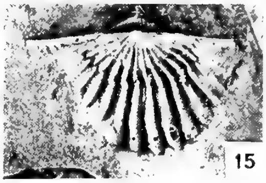
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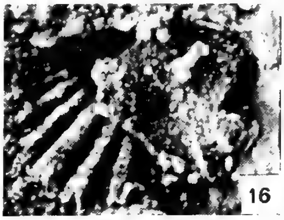
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PLATE 8

Orthis sp. (p. 51)

Stapeley Volcanic Group, Leigh, Shropshire.

FIG. 1. BB 35425. Latex cast of the interior of a brachial valve, ×6·5.

Lenorthis cf. ***proava*** (Salter) (p. 52)

Mytton Flags, Snailbeach, Shropshire.

FIGS. 3, 2. BB 35501a, b. Latex cast of the exterior and the internal mould of a pedicle valve, ×6·6, ×3·4.

FIGS. 5, 4. BB 35502a, b. Latex cast of the exterior and the internal mould of a pedicle valve, ×3·5.

Mytton Flags, Perkin's Beach, Shropshire.

FIGS, 6, 9. BB 35504a. Latex cast and mould of the interior of a brachial valve, ×3·7.

FIGS, 7, 8. BB 35503a, b. Latex cast of the exterior and interior of a brachial valve, ×3·5.

Orthambonites exopunctata sp. nov. (p. 53)

Whittery Shales, near Hockleton Bridge, Shropshire.

FIGS. 10, 11. Holotype, BB 35371. General and detailed views of the exterior of a brachial valve, ×3·3, ×10.

FIG. 12. Paratype, BB 35372. Exterior of a brachial valve, ×3·2.

FIGS. 13, 16. Paratype, BB 35376a, b. Interior and internal mould of pedicle valve, ×3·1, ×3·9.

FIG. 14. Paratype, BB 35373. Latex cast of the interior of a brachial valve, ×3·5.

Whittery Shales, Whittery Quarry, Shropshire.

FIG. 15. Paratype, BB 35375. Internal mould of a pedicle valve, ×4·2.

Whittery Shales, River Camlad, Shropshire.

FIG. 17. Paratype, BB 35374a. Latex cast of the interior of a brachial valve, ×4·7.


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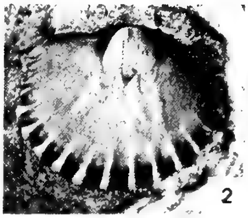
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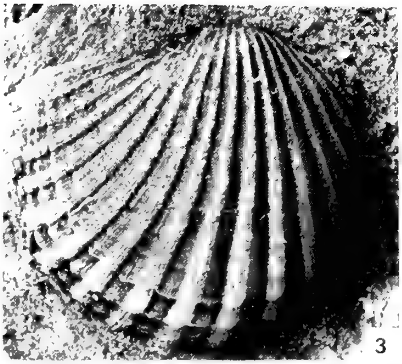
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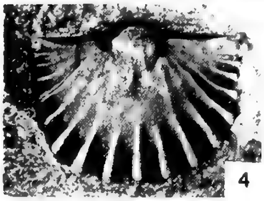
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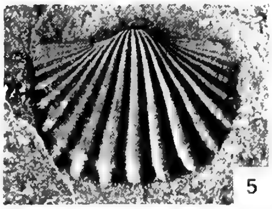
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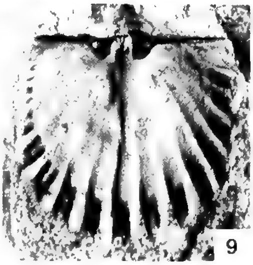
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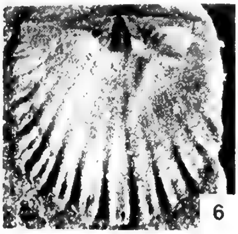
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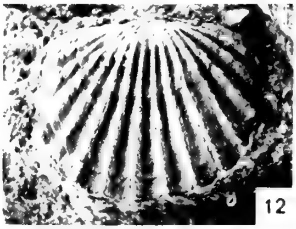
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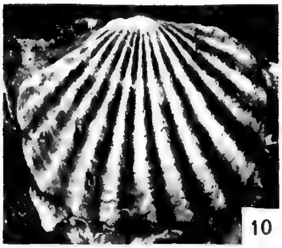
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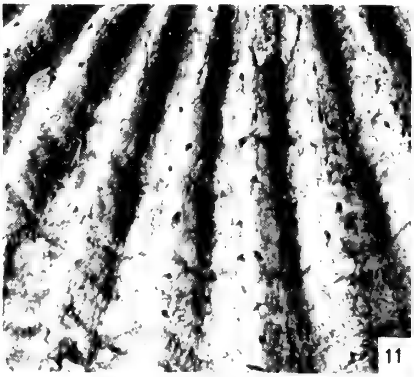
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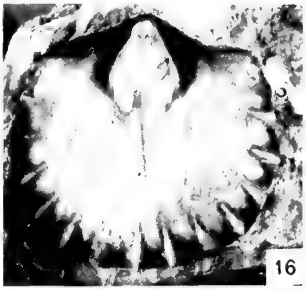
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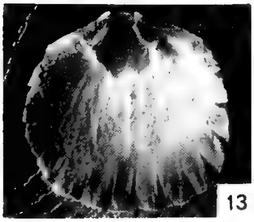
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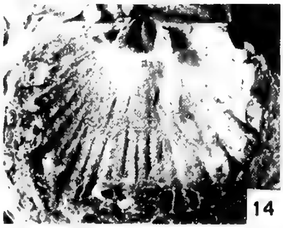
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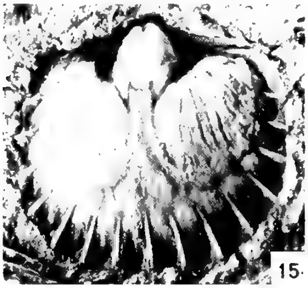
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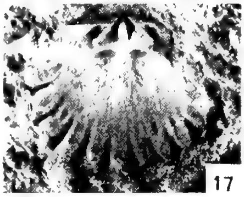
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PLATE 9

Nicolella cf. ***actoniae*** (J. de C. Sowerby) (p. 57)

Whittery Shales, Whittery Quarry, Shropshire.

FIGS. 1, 4. BB 35327a, b. Latex casts of the exterior and interior of a brachial valve, ×6.

Whittery Shales, near Hockleton Bridge, Shropshire.

FIG. 2. BB 35330. Latex cast of the interior of a pedicle valve, ×3.

Whittery Shales, River Camlad, Shropshire.

FIG. 3. BB 35328a. Latex cast of the interior of a brachial valve, ×3·2.

Whittery Shales, near Marrington Farm, Shropshire.

FIG. 5. BB 35331. Internal mould of a pedicle valve, ×2·8.
FIG. 6. BB 35329. Latex cast of the exterior of a brachial valve, ×3·2.

Whittardia paradoxica gen. et sp. nov. (p. 62)

Whittery Shales, Whittery Quarry, Shropshire.

FIGS, 7, 8. Paratype, BB 35385. Latex cast and mould of the interior of a brachial valve, ×3·6, ×4·2.

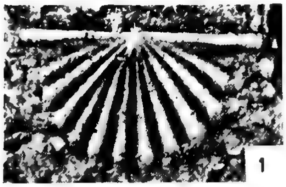
FIGS. 9, 13. Holotype, BB 35381b. Latex cast, with detail, of the exterior of a brachial valve, ×5·2, ×13.

FIG. 10. Paratype, BB 35403. Internal mould of a pedicle valve, ×5.

FIGS. 12, 11. Paratype, BB 35383b. Latex cast, with detail, of the exterior of a pedicle valve, ×5, ×12·5.

FIG. 14. Paratype, BB 35382a. Internal mould of a pedicle valve, ×2·6.

FIG. 15. Paratype, BB 35402a. Latex cast of the interior of a brachial valve, ×4·3.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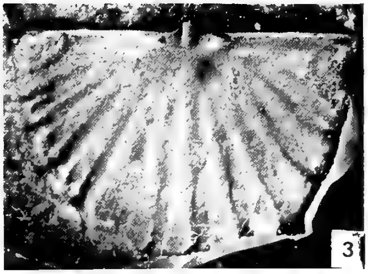
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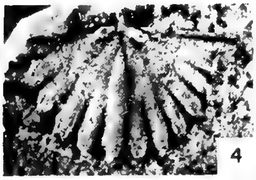
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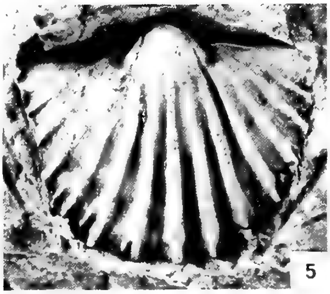
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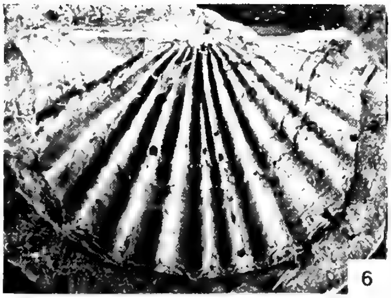
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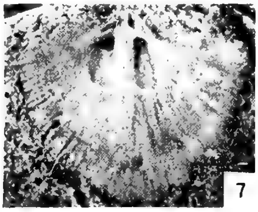
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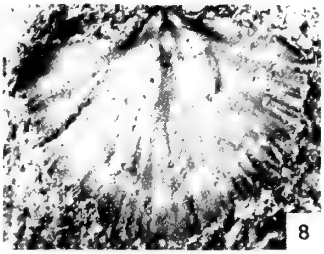
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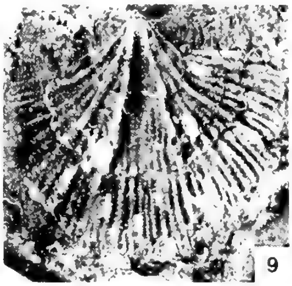
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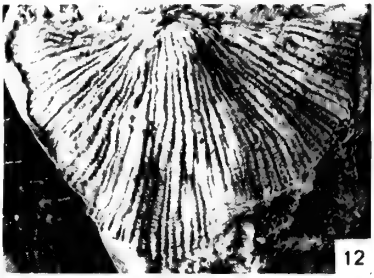
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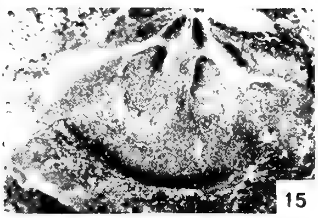
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PLATE 10

Whittardia paradoxica gen. et sp. nov. (p. 62)

Whittery Shales, near Hockleton Bridge, Shropshire.

FIG. 1. Paratype, BB 35384b. Latex cast of the exterior of a brachial valve, × 4·8.

Whittery Shales, Whittery Quarry, Shropshire.

FIG. 2. Paratype, BB 35383a. Internal mould of a pedicle valve, × 5·1.

FIG. 4. Paratype, BB 35402b. Latex cast of the exterior of a brachial valve, × 5·7.

Dolerorthis cf. ***tenuicostata*** Williams (p. 63)

Whittery Shales, Whittery Quarry, Shropshire.

FIGS. 3, 5. BB 35460a, b. Latex cast of the exterior and the internal mould of a pedicle valve, × 6·1, × 3·6.

FIGS. 7, 10, 13. BB 35459a, b. Latex casts of the exterior and the interior and the internal mould of a brachial valve, × 3·3, × 3·6, × 3·6.

Glyptorthis viriosa sp. nov. (p. 64)

Spy Wood Grit, near Rorrington, Shropshire.

FIGS. 6, 14. Holotype, BB 35505a, b. Latex casts of the exterior and interior of a brachial valve, × 5.

FIG. 8. Paratype, BB 35509. Internal mould of a pedicle valve, × 4·8.

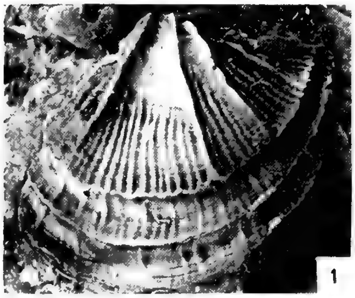
FIG. 9. Paratype, BB 35506a. Internal mould of a pedicle valve, × 5·3.

FIG. 11. Paratype, BB 35508a. Latex cast of the interior of a brachial valve, × 5.

FIG. 12. Paratype, BB 35507. Internal mould of a pedicle valve, × 5.

Meadowtown Beds, Minicop Farm, Shropshire.

FIG. 15. BB 35520b. Latex cast of the exterior of a brachial valve, × 7·5.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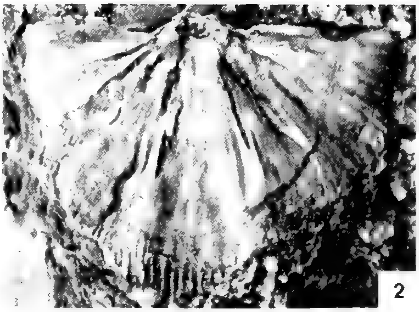
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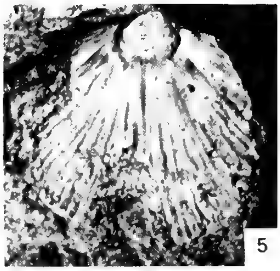
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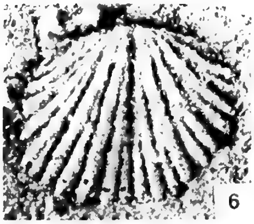
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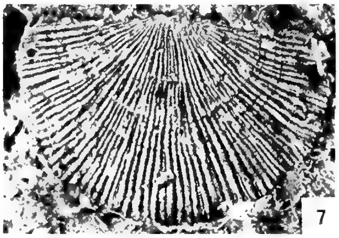
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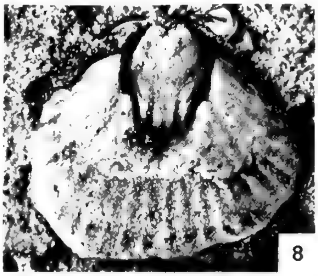
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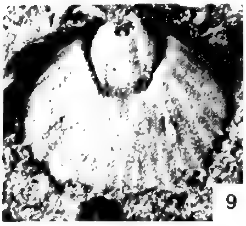
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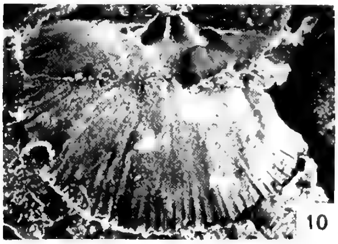
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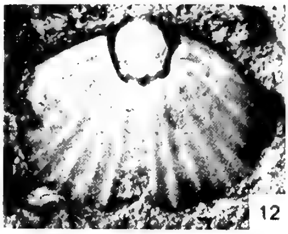
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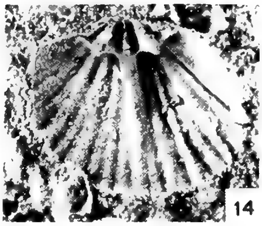
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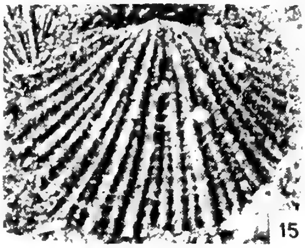
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PLATE 11

Glyptorthis viriosa sp. nov. (p. 64)

Meadowtown Beds, Quinton's Quarry, Shropshire.

FIGS. 1, 2. BB 35521a, b. Latex cast of the exterior and the internal mould of a pedicle valve, ×6·8, ×5·1.

Meadowtown Beds, Minicop Farm, Shropshire.

FIG. 4. BB 35520a. Internal mould of a brachial valve, ×5·5.

Diparelasma sp. (p. 71)

Mytton Flags, near Mytton's Beach, Shropshire.

FIG. 3. BB 35335a, b. Latex casts of the interior of a brachial valve and the exterior of the complementary pedicle valve, ×8.

Mytton Flags, near Blakemoorflat, Shropshire.

FIGS. 7, 8. BB 35336a, b. Latex casts of the exterior and interior of a brachial valve, ×5.

Astraborthis uniplicata gen. et sp. nov. (p. 70)

Mytton Flags, near Snailbeach Reservoir, Shropshire.

FIGS. 6, 5, 11. Paratype, BB 35325a, b. Latex casts of the exterior and interior and the internal mould of a brachial valve, ×4·7, ×4, ×4.

FIGS. 14, 9. Holotype, BB 35324a, b. Latex cast of part of the exterior and the internal mould of a pedicle valve, ×4, ×2·8.

Plectorthis sp. (p. 73)

Aldress Shales, Ox Wood Dingle, Shropshire.

FIGS. 15, 12. BB 35466a. Latex cast and mould of the interior of a pedicle valve, ×2·7.

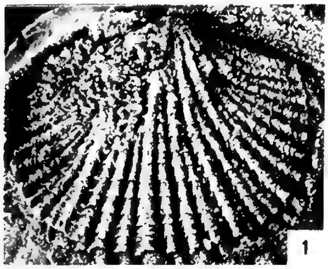
Plectorthis whitteryensis sp. nov. (p. 71)

Whittery Shales, River Camlad, Shropshire.

FIGS. 13, 10. Holotype, BB 35462a, b. Latex cast of the exterior and the internal mould of a pedicle valve, ×3·4.

FIG. 16. Paratype, BB 37158a. Internal mould of a pedicle valve, ×3·5.

FIG. 17. Paratype, BB 35463a. Internal mould of a brachial valve, ×3·5.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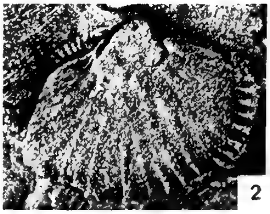
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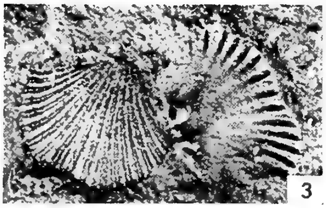
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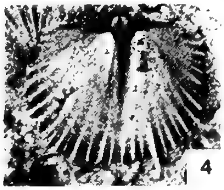
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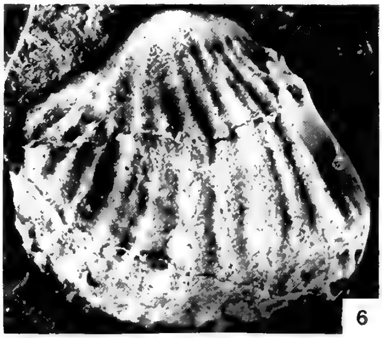
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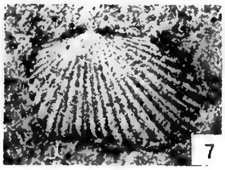
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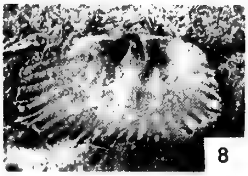
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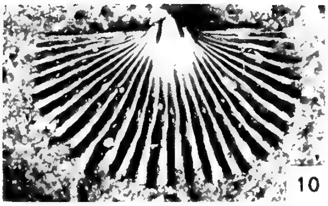
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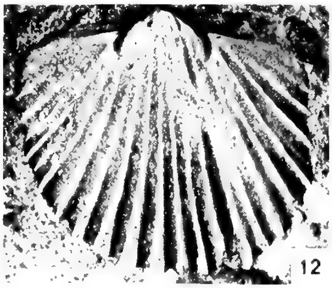
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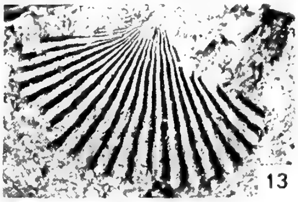
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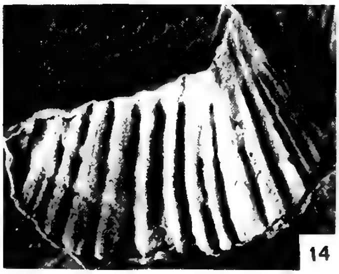
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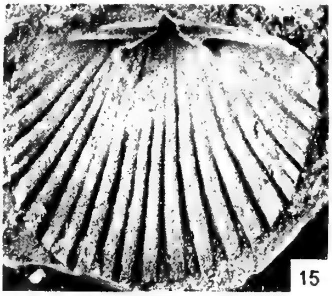
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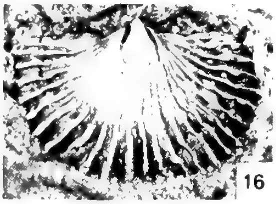
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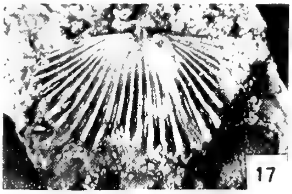
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PLATE 12

Plectorthis whitteryensis sp. nov. (p. 71)

Whittery Shales, River Camlad, Shropshire.

FIG. 1. Paratype, BB 35464a. Latex cast of the interior of a brachial valve, ×3·5.

Desmorthis ? sp. nov. (p. 73)

Stapeley Volcanic Group, Perkin's Beach, Shropshire.

FIG. 2. BB 35339a. Internal mould of pedicle valve, ×5.

FIG. 3. BB 35338a. Internal mould of pedicle valve, ×6·3.

Mytton Flags, near Blakemoorflat, Shropshire.

FIGS. 8, 4. BB 35337a, b. Latex casts of the exterior and interior of a brachial valve, ×4, ×3.

Gelidorthis cf. ***partita*** (Barrande) (p. 74)

Rorrington Beds, Spy Wood Brook, Shropshire.

FIG. 5. BB 35419a. Internal mould of a brachial valve, ×7.

FIG. 6. BB 35418a. Internal mould of a pedicle valve, ×5.

FIG. 7. BB 37159a. Internal mould of a pedicle valve, ×5.

Tazzarinia elongata sp. nov. (p. 75)

Meadowtown Beds, near Waitchley, Shropshire.

FIGS. 9, 11, 10. Holotype, BB 35332a, b. Latex casts of the exterior and interior and the internal mould of a brachial valve, ×5·5, ×6·2, ×5.

FIGS. 12, 15. Paratype, BB 35333a, b. Latex cast of the exterior and the internal mould of a pedicle valve, ×6·1.

Platystrophia caelata sp. nov. (p. 76)

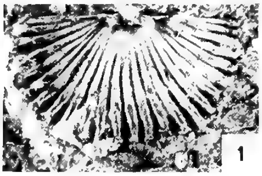
Whittery Shales, River Camlad, Shropshire.

FIGS. 16, 13. Paratype, BB 35495a, b. Latex cast of the exterior and the internal mould of a pedicle valve, ×4, ×2·5.

FIG. 17. Paratype, BB 35494a. Internal mould of a pedicle valve, ×2·7.

Whittery Shales, Whittery Quarry, Shropshire.

FIGS. 19, 14, 18. Holotype, BB 35493a, b. Latex cast and detail of the mould of the exterior and the internal mould of a brachial valve, ×2·6, ×14, ×2·6.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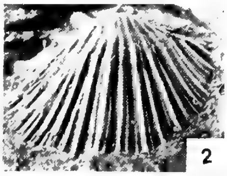
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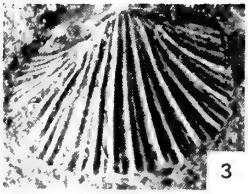
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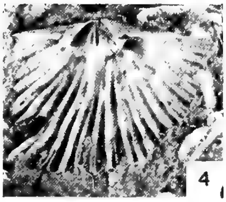
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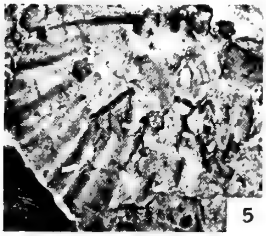
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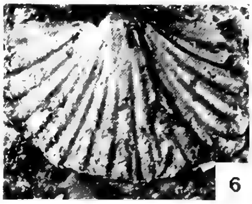
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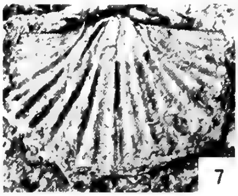
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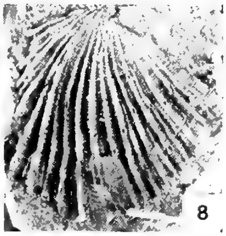
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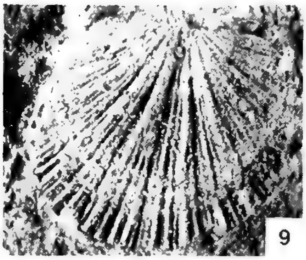
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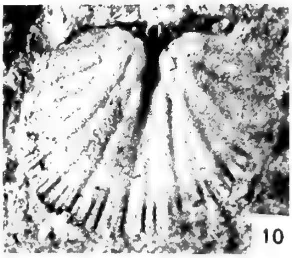
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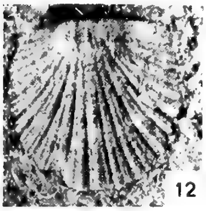
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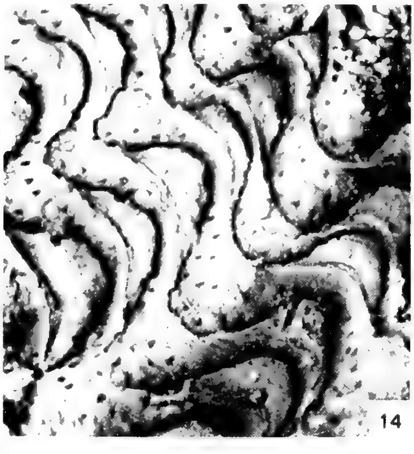
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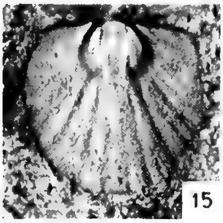
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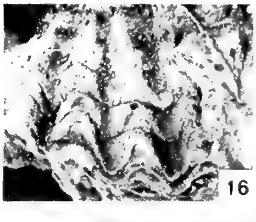
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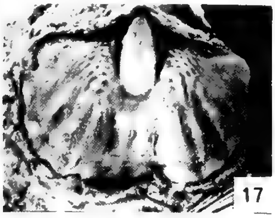
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PLATE 13

Platystrophia cf. ***major*** Williams (p. 78)

Aldress Shales, Ox Wood Dingle, Shropshire.

FIG. 1. BB 35586a. Internal mould of a brachial valve, ×7.

Spy Wood Grit, near Rorrington, Shropshire.

FIGS. 4, 2. BB 35587a, b. Latex cast of the exterior and the internal mould of a pedicle valve, ×6·2.

Mcewanella sp. (p. 78)

Whittery Shales, near Hockleton Bridge, Shropshire.

FIG. 3. BB 35417. Internal mould of a pedicle valve, ×2·1.

FIG. 5. BB 35416. Exterior of a pedicle valve, ×2·4.

Salacorthis costellata gen. et sp. nov. (p. 80)

Spy Wood Grit, near Rorrington, Shropshire.

FIGS. 7, 11, 6, 10. Holotype, BB 37153a, b. Latex casts and moulds of the exterior and interior of a brachial valve, ×7·6, ×4·9, ×7·6, ×7·6.

FIG. 8. Paratype, BB 37154. Internal mould of a pedicle valve, ×3·1.

FIG. 12. Paratype, BB 37155. Latex cast of the exterior of a brachial valve, ×3·6.

FIG. 13. Paratype, BB 37157. Latex cast of the exterior of a brachial valve, ×5·1.

Spy Wood Grit, Spy Wood Brook, Shropshire.

FIG. 9. Paratype, BB 37156. Latex cast of the exterior of a brachial valve, ×6.

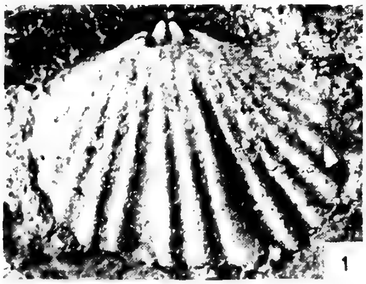
Skenidioides cf. ***costatus*** Cooper (p. 82)

Spy Wood Grit, Spy Wood Brook, Shropshire.

FIG. 14. BB 35413. Latex cast of the exterior of a pedicle valve, ×12.

Whittery Shales, River Camlad, Shropshire.

FIGS. 16, 15. BB 35409. Latex cast and mould of the interior of a brachial valve, ×5·7, ×7.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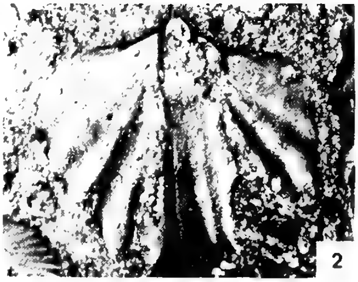
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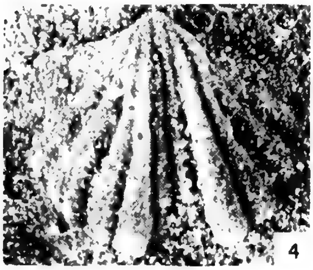
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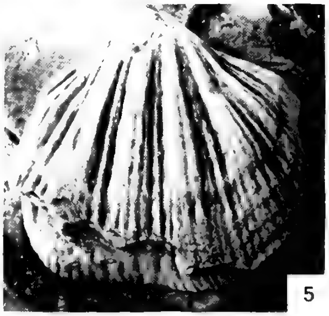
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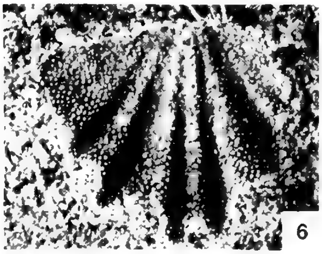
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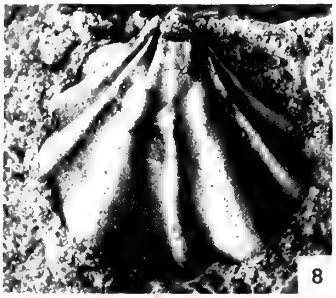
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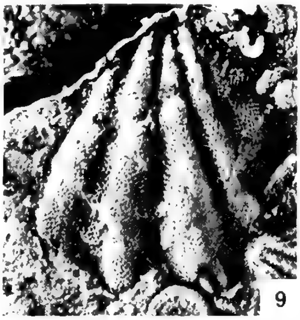
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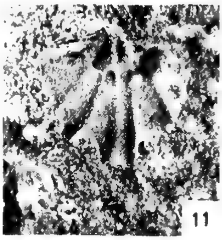
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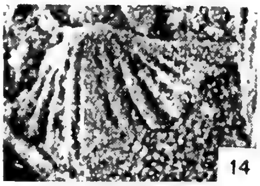
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PLATE 14

Skenidioides cf. ***costatus*** Cooper (p. 82)

Whittery Shales, Hockleton Bridge, Shropshire.

FIG. 1. BB 35410. Internal mould of a pedicle valve, × 7·2.

Spy Wood Grit, Spy Wood Brook, Shropshire.

FIG. 2. BB 35411. Internal mould of a pedicle valve, × 13·3.

FIG. 3. BB 35412. Internal mould of a pedicle valve, × 12·5.

Protoskenidioides revelata gen. et sp. nov. (p. 85)

Mytton Flags, near Gravels, Shropshire.

FIG. 4. Paratype, BB 35395a. Internal mould of a pedicle valve, × 13·6.

FIG. 9. Paratype, BB 35394b. Latex cast of the exterior of a brachial valve, × 10.

FIG. 11. Paratype, BB 35397b. Latex cast of the exterior of a brachial valve, × 12·5.

FIGS. 12, 6. Paratype, BB 35400a. Latex cast and mould of the interior of a brachial valve, × 9, × 14.

Mytton Flags, near Shelve Church, Shropshire.

FIG. 5. Holotype, BB 35387. Internal mould of a brachial valve, × 12·4.

FIG. 7. Paratype, BB 35389. Internal mould of a pedicle valve, × 15.

FIG. 8. Paratype, BB 35399a. Internal mould of a brachial valve, × 14.

FIG. 10. Paratype, BB 35393. Internal mould of a brachial valve, × 14·5.

FIG. 13. Paratype, BB 35398a. Internal mould of a brachial valve, × 10.

Drabovia cf. ***fascicostata*** Havlíček (p. 87)

Spy Wood Grit, near Rorrington, Shropshire.

FIG. 14. BB 35319b. Latex cast of the exterior of a pedicle valve, × 7·1.

FIGS. 15, 18. BB 35316a, b. Latex casts of the exterior and interior of a brachial valve, × 8.

FIG. 16. BB 35317a. Internal mould of a brachial valve, × 6·4.

FIG. 19. BB 35318a. Internal mould of a pedicle valve, × 6·7.

Nocturniella sp. (p. 88)

Mytton Flags, Snailbeach, Shropshire.

FIGS. 17, 20. BB 35341. Latex cast and mould of the interior of a brachial valve, × 7.


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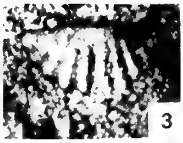
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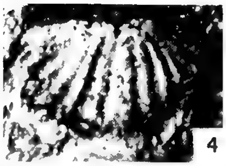
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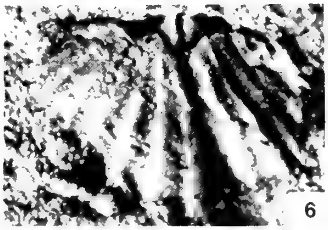
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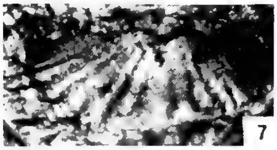
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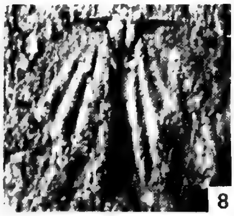
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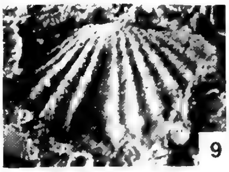
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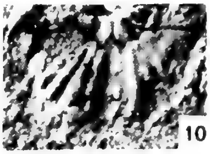
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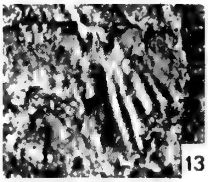
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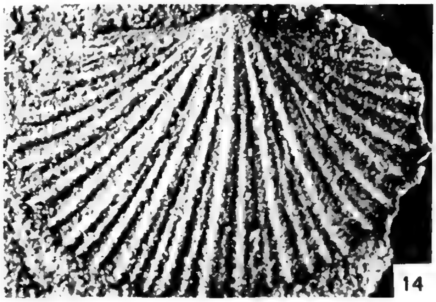
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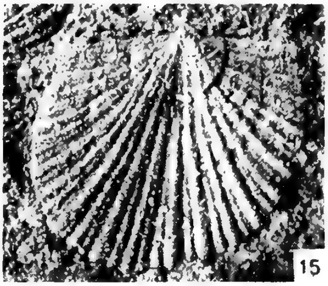
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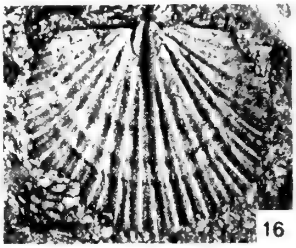
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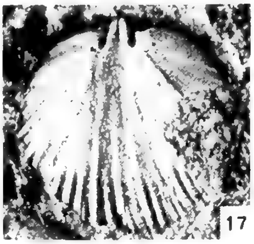
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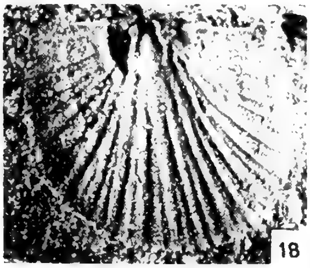
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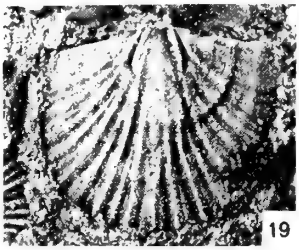
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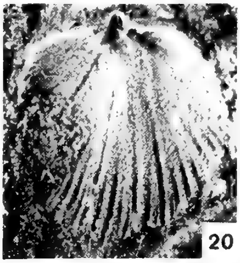
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PLATE 15

Dalmanella parva Williams (p. 89)

Lower Llandeilo sandstones, near Ysgubor-wen Farm, Llandeilo, Carmarthenshire.

FIG. 1. BB 35436. Internal mould of a brachial valve, ×8.

FIG. 2. BB 35437. Latex cast of the exterior of a brachial valve, ×6.

FIGS, 3, 7. BB 35434. Latex cast and mould of the interior of a brachial valve, ×6·5.

FIG. 4. BB 35435. Internal mould of a pedicle valve, ×6·9.

Dalmanella salopiensis sp. nov. (p. 90)

Meadowtown Beds, near Minicop Farm, Shropshire.

FIGS. 8, 5. Holotype, BB 35446a, b. Latex cast of the exterior and the internal mould of a brachial valve, ×8, ×6.

FIG. 11. Paratype, BB 35448a. Internal mould of a brachial valve, ×6·3.

Meadowtown Beds, Quinton's Quarry, Shropshire.

FIGS. 12, 6. Paratype, BB 35450a, b. Latex casts of the exterior and interior of a brachial valve, ×7·2.

Meadowtown Beds, near Meadowtown Chapel, Shropshire.

FIGS. 10, 9. Paratype, BB 35447a, b. Latex cast of the exterior and the internal mould of a pedicle valve, ×6·9, ×7·8.

Dalmanella salopiensis gregaria sp. et subsp. nov. (p. 91)

Spy Wood Grit, Spy Wood Brook, Shropshire.

FIGS. 16, 13. Holotype, BB 35443a, b. Latex cast of the exterior and the internal mould of a brachial valve, ×6·4, ×7·5.

FIG. 14. Paratype, BB 35407a. Internal mould of a pedicle valve, ×7·3.

FIG. 15. Paratype, BB 35444a. Internal mould of a pedicle valve, ×9.

FIG. 20. Paratype, BB 35445a. Latex cast of the interior of a brachial valve, ×10.

Dalmanella salopiensis transversa sp. et subsp. nov. (p. 92)

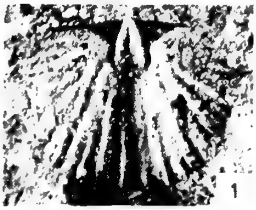
Aldress Shales, Ox Wood Dingle, Shropshire.

FIGS. 21, 19. Holotype, BB 35438a, b. Latex casts of the exterior and interior of a brachial valve, ×6·5.

FIGS. 22, 23. Paratype, BB 35441a, b. Latex cast of the exterior and the internal mould of a pedicle valve, ×10.

FIG. 24. Paratype, BB 35439a. Internal mould of a pedicle valve, ×6·9.

FIGS. 18, 17. Paratype, 35440a, b. Latex cast of the exterior and the internal mould of a brachial valve, ×10.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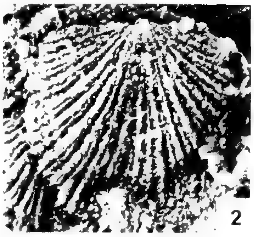
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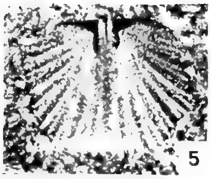
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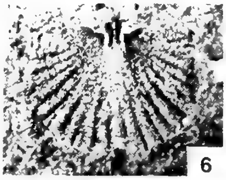
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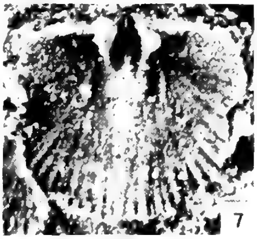
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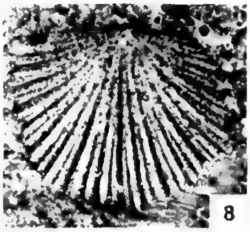
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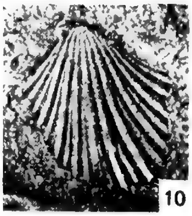
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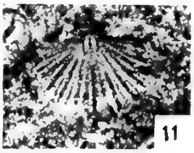
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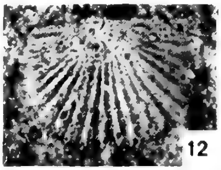
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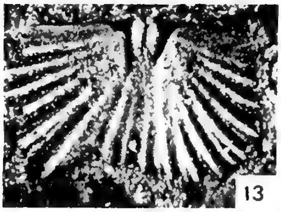
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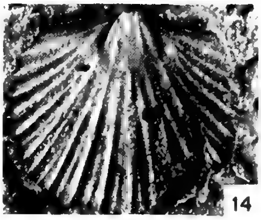
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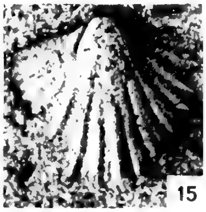
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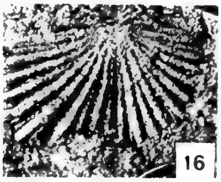
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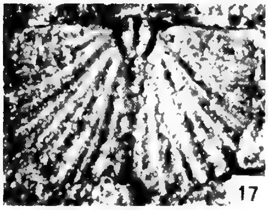
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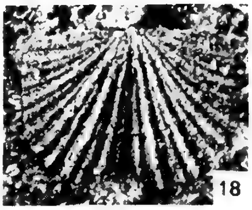
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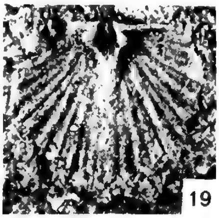
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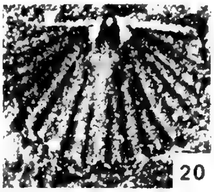
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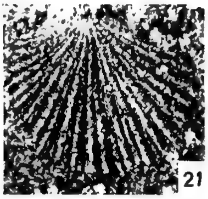
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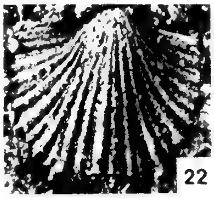
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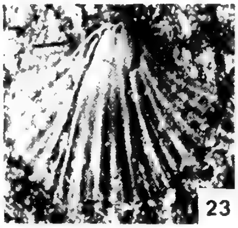
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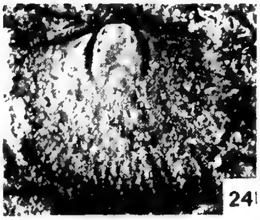
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PLATE 16

Dalmanella salopiensis transversa sp. et subsp. nov. (p. 92)

Aldress Shales, Ox Wood Dingle, Shropshire.

FIG. 1. Paratype, BB 35442a. Internal mould of a pedicle valve, × 10.

Dalmanella elementaria sp. nov. (p. 97)

Mytton Flags, near Shelve Church, Shropshire.

FIGS. 2, 3. Holotype, BB 35352a, b. Latex cast of the exterior and the internal mould of a brachial valve, × 7·8.

FIG. 4. Paratype, BB 35357a. Internal mould of a brachial valve, × 8.

FIG. 7. Paratype, BB 35355a. Internal mould of a brachial valve, × 8·3.

FIG. 8. Paratype, BB 35356a. Internal mould of a brachial valve, × 8.

Mytton Flags, near Wood House, Shropshire.

FIGS. 5, 6. Paratype, BB 35353a, b. Latex cast of the exterior and the internal mould of a pedicle valve, × 8.

Onniella ostentata lepida subsp. nov. (p. 98)

Aldress Shales, Ox Wood Dingle, Shropshire.

FIG. 9. Paratype, BB 35457a. Internal mould of a brachial valve, × 5·7.

FIGS. 10, 11. Holotype, BB 35456a, b. Latex cast of the exterior and the internal mould of a brachial valve, × 7, × 5·6.

FIG. 12. Paratype, BB 35458. Latex cast of the interior of a brachial valve, × 8.

FIGS. 13, 14. Paratype, BB 35455a, b. Latex cast of the exterior and the internal mould of a pedicle valve, × 6·0, × 5·8.

Onniella sp. (p. 99)

Spy Wood Grit, Shropshire (unlocated exposure).

FIGS. 15, 18. BB 35572a, b. Latex casts of the exterior and interior of a brachial valve, × 6.

Harknessella cf. ***subplicata*** Bancroft (p. 102)

Spy Wood Grit, near Rorrington, Shropshire.

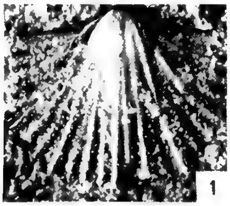
FIG. 16. BB 35427. Internal mould of a brachial valve, × 6·7.

Horderleyella cf. ***plicata*** Bancroft (p. 102)

Spy Wood Grit, near Rorrington, Shropshire.

FIG. 17. BB 35432. Internal mould of a brachial valve, × 6·6.

FIGS. 19, 20. BB 35431a, b. Latex cast of the exterior and the internal mould of a pedicle valve, × 4.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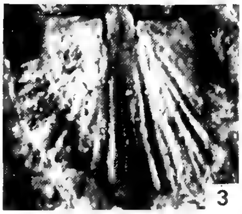
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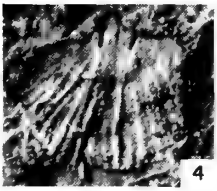
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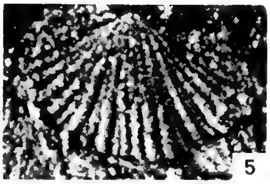
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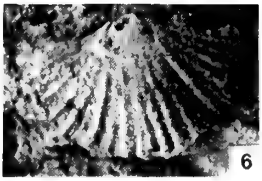
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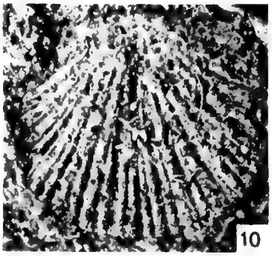
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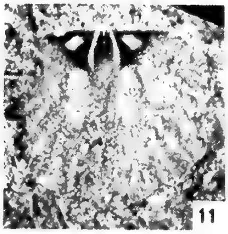
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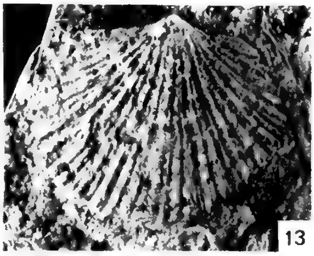
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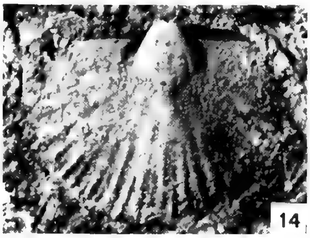
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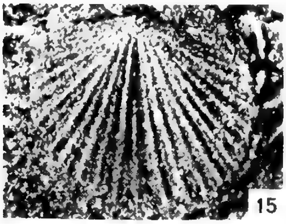
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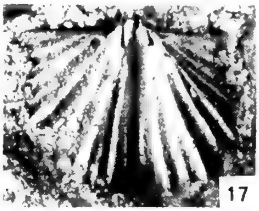
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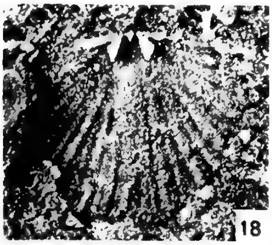
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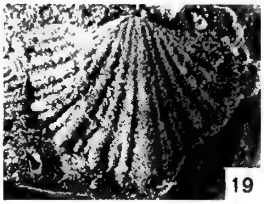
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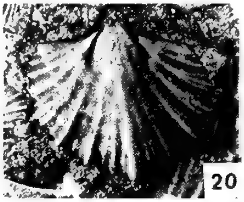
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PLATE 17

Horderleyella cf. ***plicata*** Bancroft (p. 102)

Aldress Shales, Ox Wood Dingle, Shropshire.

FIG. 1. BB 35433. Internal mould of a brachial valve, ×4·5.

Horderleyella sp. (p. 104)

Meadowtown Beds, near Meadowtown Chapel, Shropshire.

FIGS. 2, 3. BB 35420a, b. Internal mould and latex cast of the exterior of a pedicle valve, ×7·5.

Reuschella horderleyensis carinata subsp. nov. (p. 104)

Whittery Shales, near Marrington Farm, Shropshire.

FIG. 4. Paratype, BB 35519a. Internal mould of a brachial valve, ×6.

Whittery Shales, River Camlad, Shropshire.

FIG. 5. Holotype, BB 35513a. Internal mould of a pedicle valve, ×2·1.
FIG. 6. Paratype, BB 35517a. Internal mould of a pedicle valve, ×1·9.
FIG. 7. Paratype, BB 35515. Latex cast of the exterior of a pedicle valve, ×2·1.
FIG. 8. Paratype, BB 35514a. Internal mould of a brachial valve, ×2·6.
FIG. 9. Paratype, BB 35518a. Latex cast of the interior of a brachial valve, ×2.

Heterorthis sp. (p. 106)

Spy Wood Grit, near Rorrington, Shropshire.

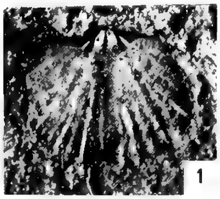
FIGS, 10, 14, 12. BB 35424a, b. Latex casts of the exterior and interior and the internal mould of a brachial valve, ×8, ×6, ×4·9.

FIGS. 11, 13. BB 35423a, b. Latex cast of the exterior and the internal mould of a pedicle valve, ×6.

Tissintia prototypa Williams (p. 108)

Lower Llanvirn ashy shales, near Llwyn Bedw Farm, Llandeilo, Carmarthenshire.

FIG. 15. BB 35310. Latex cast of the interior of a brachial valve, ×3·2.
FIG. 16. BB 35305. Latex cast of the interior of a brachial valve, ×3·3.
FIGS. 18, 17. BB 35309. Latex cast and internal mould of a brachial valve, ×2·3.
FIG. 19. BB 35308. Latex cast of the exterior of a brachial valve, ×3·5.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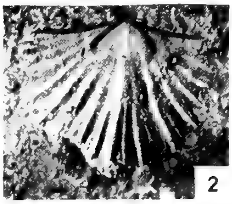
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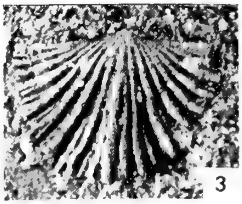
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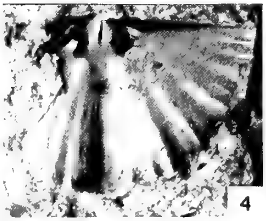
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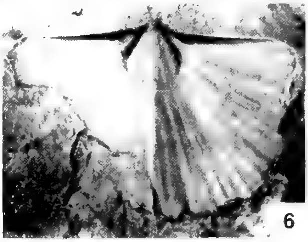
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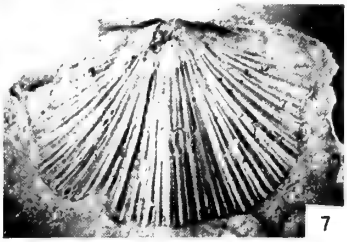
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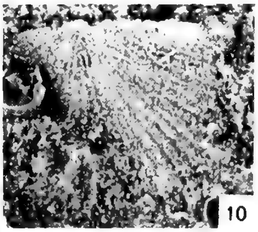
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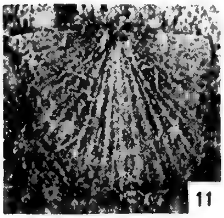
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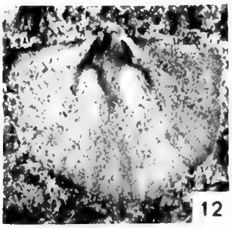
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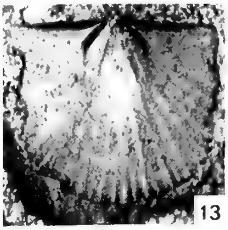
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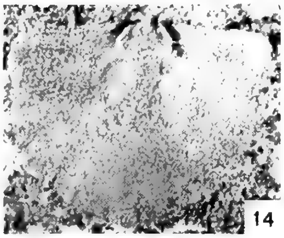
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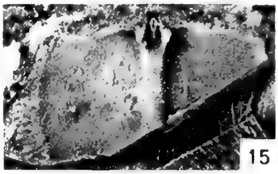
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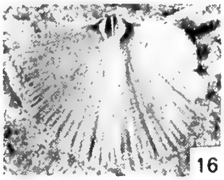
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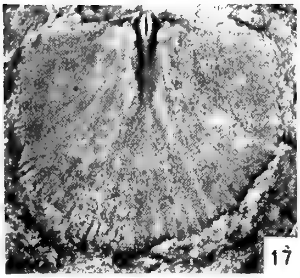
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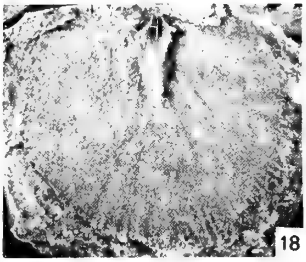
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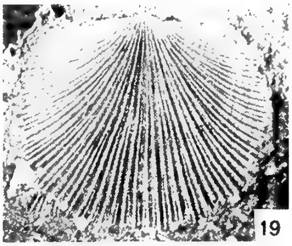
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PLATE 18

Tissintia prototypa (Williams) (p. 108)

Lower Llanvirn ashy shales, near Llwyn Bedw Farm, Llandeilo, Carmarthenshire.

FIG. 1. BB 35306. Internal mould of a pedicle valve, × 3.

FIG. 2. BB 35307. Latex cast of the exterior of a brachial valve, × 3·3.

Weston Beds, near Lyde, Shropshire.

FIGS. 11, 3. BB 35311a, b. Latex cast of the exterior and the internal mould of a pedicle valve, × 1·9, × 2·4.

FIG. 6. BB 35315a. Latex cast of the interior of a brachial valve, × 2·5.

FIGS. 8, 7. BB 35314a. Latex cast and internal mould of a brachial valve, × 2·2.

Weston Beds, near Priestweston, Shropshire.

FIGS. 5, 4. BB 35312a. Latex cast and mould of the interior of a pedicle valve, × 2·6.

Weston Beds, near Little Weston, Shropshire.

FIG. 9. BB 35313b. Latex cast of the exterior of a brachial valve, × 2.

Tissintia immatura (Williams) (p. 109)

Meadowtown Beds, Quinton's Quarry, Shropshire.

FIG. 10. BB 35479. Internal mould of a pedicle valve, × 2·7.

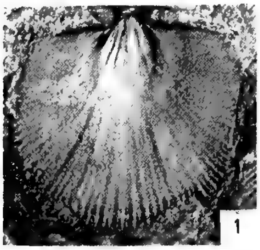
Meadowtown Beds, near Meadowtown, Shropshire.

FIG. 12. BB 35477a. Latex cast of the internal mould of a brachial valve, × 2.

FIG. 15. BB 35476b. Latex cast of the exterior of a pedicle valve, × 3·8.

Meadowtown Beds, Minicop Farm, Shropshire.

FIGS. 13, 14. BB 35474a, b. Latex cast of the exterior and the internal mould of a pedicle valve, × 2, × 2·5.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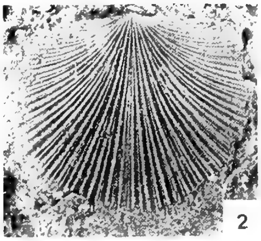
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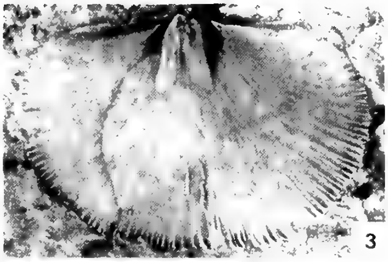
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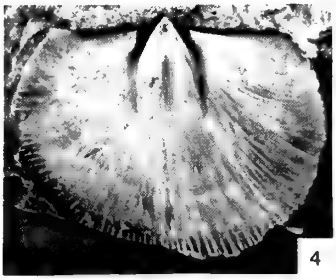
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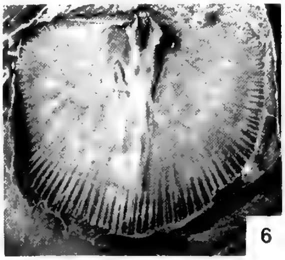
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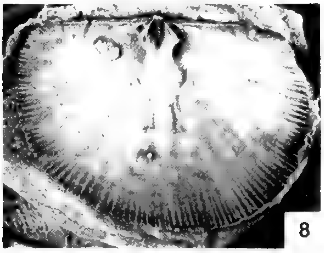
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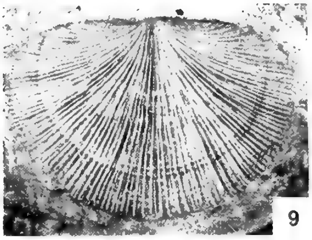
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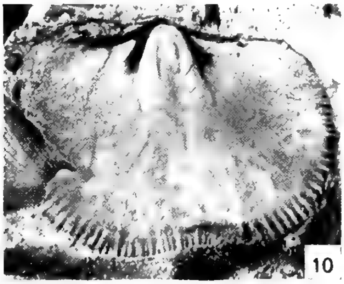
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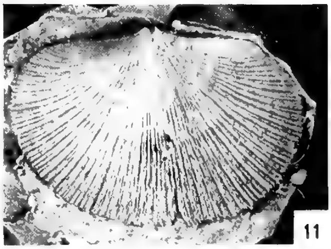
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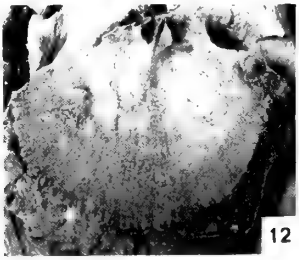
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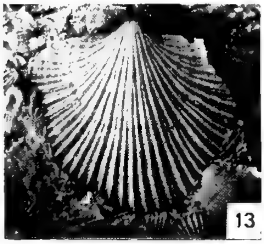
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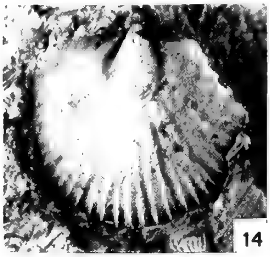
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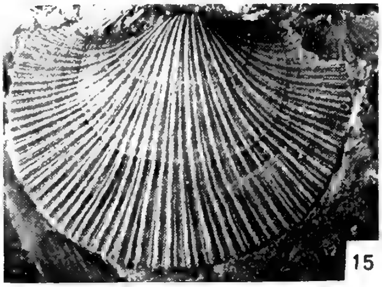
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PLATE 19

Tissintia immatura (Williams) (p. 109)

Meadowtown Beds, Meadowtown Quarry, Shropshire.

FIGS. 1, 2, 5. B 35478a, b. Latex casts of the exterior and interior and the internal mould of a brachial v ×3·8, ×3·5, ×2·5.

Meadowtown Beds, Minicop Farm, Shropshire.

FIGS. 3, 4. BB 35475a, b. Latex cast of the exterior and the internal mould of a brachial valve, ×2·5.

Salopia sp. (p. 114)

Whittery Shales, Whittery Quarry, Shropshire.

FIGS. 9, 6. BB 35428a, b. Latex cast of the exterior and the internal mould of a brachial valve, ×4·6, ×3·5.

FIG. 8. BB 35429a. Internal mould of pedicle valve, ×2·9.

Whittery Shales, near Hockleton Bridge, Shropshire.

FIG. 7. BB 35430a. Internal mould of pedicle valve, ×3.

Salopia cf. ***salteri*** (Davidson) (p. 114)

Spy Wood Grit, near Rorrington, Shropshire.

FIGS. 10, 11. BB 35426a. Latex cast and mould of the interior of a brachial valve, ×4·2, ×5.

Oslogonites ? sp. (p. 115)

Mytton Flags, near Wood House, Shropshire.

FIGS. 12, 13. BB 35326a, b. Latex cast of the exterior and the internal mould of a brachial valve, ×10.

Kullervo sp. (p. 115)

Meadowtown Beds, near Meadowtown Chapel, Shropshire.

FIGS. 15, 14. BB 35340a, b. Latex cast of the exterior and the internal mould of a pedicle valve, ×8, ×5·5.

Triplesia sp. (p. 116)

Whittery Shales, near Hockleton Bridge, Shropshire.

FIG. 16. BB 35408. Internal mould of a pedicle valve, ×2·5.

Bicuspina subquadrata sp. nov. (p. 117)

Whittery Shales, Whittery Quarry, Shropshire.

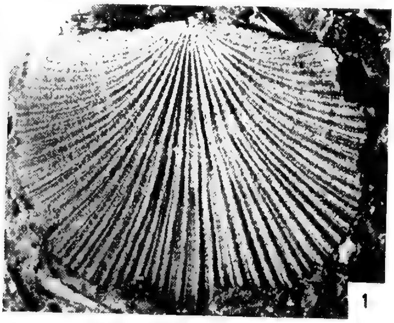
FIG. 17. Paratype, BB 35481b. Latex cast of the exterior of a brachial valve, ×2·1.

FIG. 19. Paratype, BB 35483. Internal mould of a brachial valve, ×1·9.

Whittery Shales, River Camlad, Shropshire.

FIG. 18. Holotype, BB 35480a. Internal mould of a pedicle valve, ×1·6.

PLATE 19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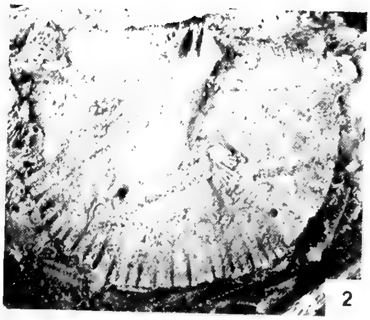
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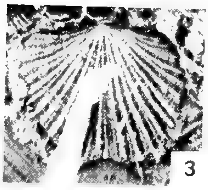
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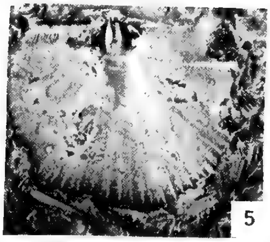
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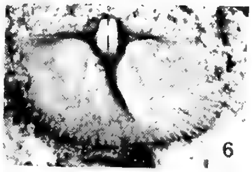
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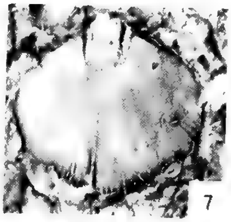
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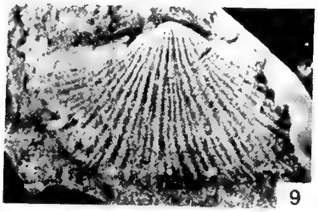
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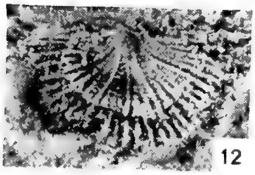
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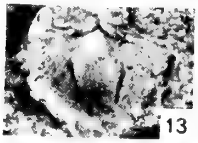
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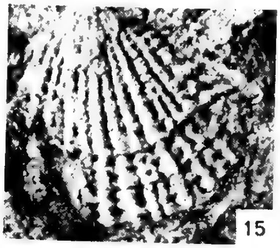
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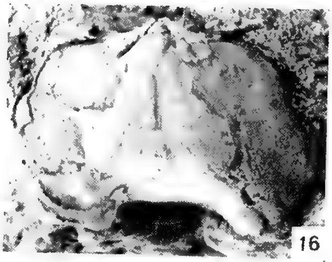
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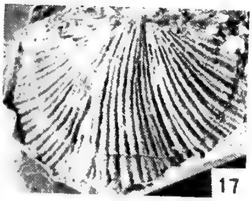
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PLATE 20

Bicuspina subquadrata sp. nov. (p. 117)

Whittery Shales, Whittery Quarry, Shropshire.

FIGS. 1, 2. Paratype, BB 35482a, b. Latex cast of the exterior and the internal mould of a pedicle valve, × 2·8.

Bicuspina modesta sp. nov. (p. 118)

Spy Wood Grit, near Rorrington, Shropshire.

FIGS. 3, 4. Paratype, BB 35512a, b. Latex cast of the exterior and the internal mould of a brachial valve, × 3·4.

FIGS. 5, 6. Holotype, BB 35510a, b. Latex cast of the exterior and the internal mould of a pedicle valve, × 3·2, × 3·5.

FIGS. 7, 8. Paratype, BB 35511a, b. Latex cast of the exterior and the internal mould of a brachial valve, × 3·3.

Oxoplecia cf. ***nantensis*** MacGregor (p. 125)

Meadowtown Beds, near Waitchley, Shropshire.

FIGS. 10, 9. BB 35320a, b. Latex cast of the exterior and the internal mould of a pedicle valve, × 3.

FIG. 12. BB 35321. Internal mould of a brachial valve, × 4·5.

FIG. 13. BB 35323. Latex cast of the interior of a brachial valve, × 5.

Meadowtown Beds, near Little Weston, Shropshire.

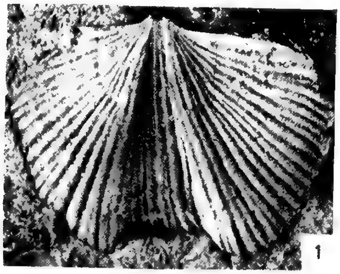
FIG. 11. BB 35322a. Internal mould of a brachial valve, × 3·5.

Caeroplecia plicata gen. et sp. nov. (p. 122)

Whittery Shales, Whittery Quarry, Shropshire.

FIGS. 15, 14. Paratype, BB 35349a, b. Latex cast of the exterior and the internal mould of a brachial valve, × 3.

FIG. 16. Paratype, BB 35351b. Latex cast of the exterior of a brachial valve, × 3·2.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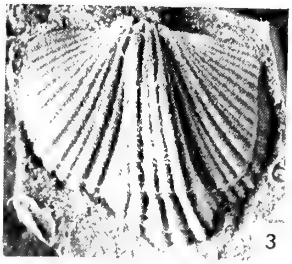
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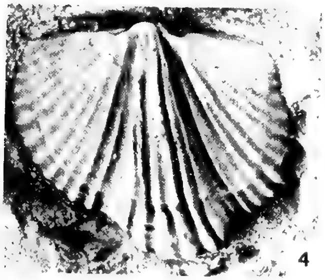
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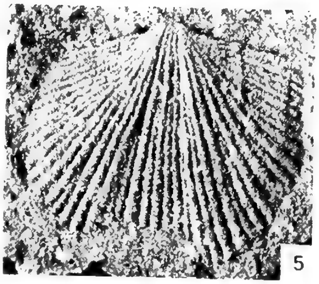
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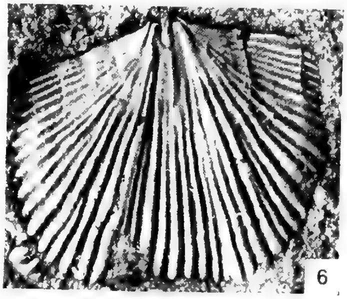
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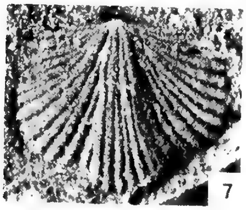
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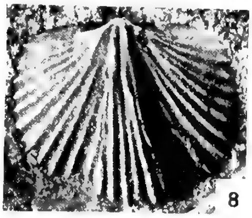
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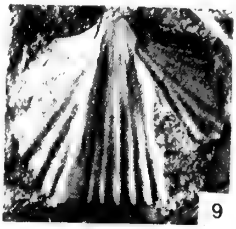
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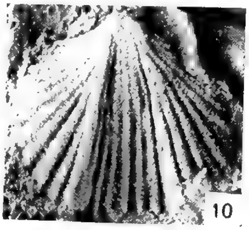
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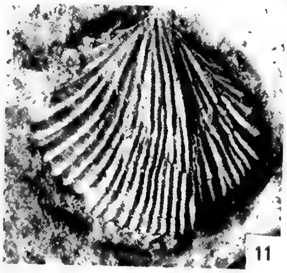
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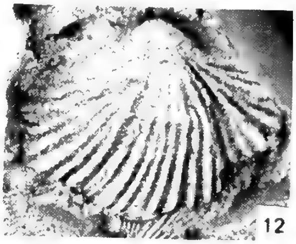
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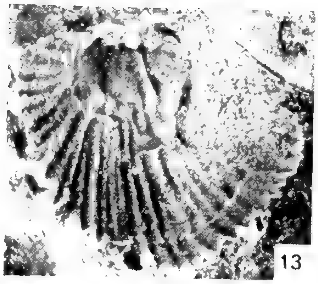
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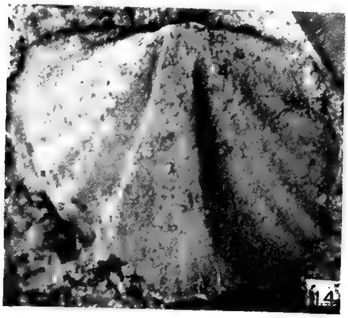
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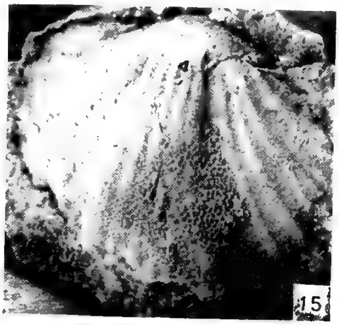
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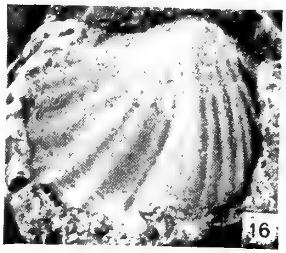
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PLATE 21

Caeroplecia plicata gen. et sp. nov. (p. 122)

Whittery Shales, Whittery Quarry, Shropshire.

FIGS. 1, 2. Holotype, BB 35342b. Latex cast, with detail, of the exterior of a pedicle valve, × 4·6, × 14.

FIG. 4. Paratype, BB 35346a. Internal mould of a pedicle valve, × 3·4.

FIGS. 8, 6. Paratype, BB 35348a, b. Latex casts of the exterior and interior of a brachial valve, × 2·6, × 2·1.

Whittery Shales, near Hockleton Bridge, Shropshire.

FIG. 3. Paratype, BB 35347a. Internal mould of a pedicle valve, × 3.

Whittery Shales, River Camlad, Shropshire.

FIG. 5. Paratype, BB 35350a. Internal mould of a brachial valve, × 4·6.

Palaeostrophomena sp. (p. 126)

Whittery Shales, Whittery Quarry, Shropshire.

FIGS. 7, 13. BB 35414a, b. Latex casts of the exterior of a pedicle and the complementary brachial valve, × 4.

Whittery Shales, near Marrington Farm, Shropshire.

FIG. 10. BB 35415a. Internal mould of a pedicle valve, × 4.

Whittery Shales, River Camlad, Shropshire.

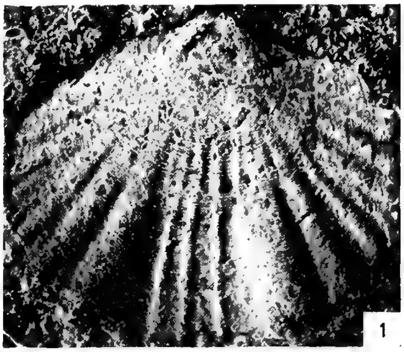
FIG. 11. BB 35451a. Internal mould of a pedicle valve, × 2·5.

Eocramatia dissimulata gen. et sp. nov. (p. 129)

Hope Shales, Brithdir Farm, Shropshire.

FIGS. 14, 9. Holotype, BB 35488a. Latex cast and mould of the interior of a pedicle valve, × 3·5.

FIGS. 12, 15. Paratype, BB 35490a. Latex cast and mould of the interior of a pedicle valve, × 3·5, × 5·5.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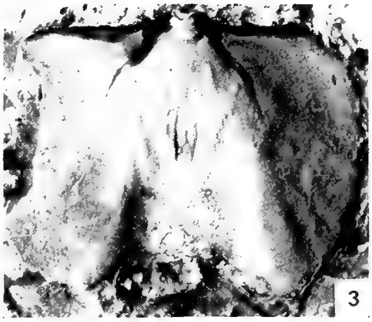
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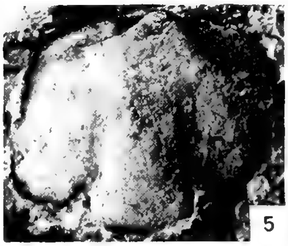
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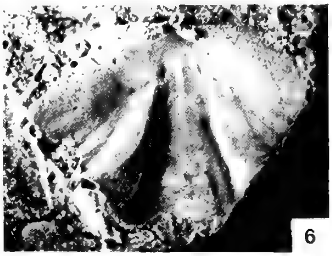
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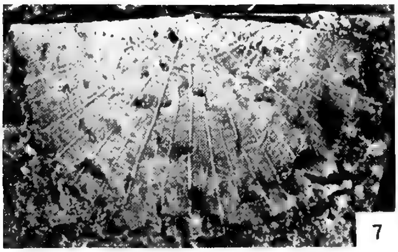
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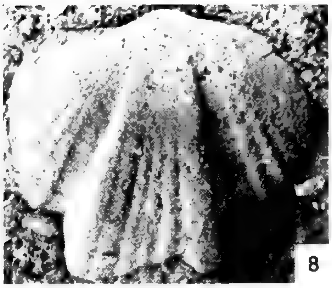
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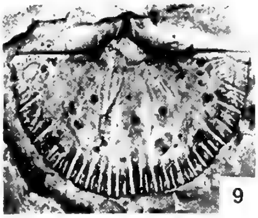
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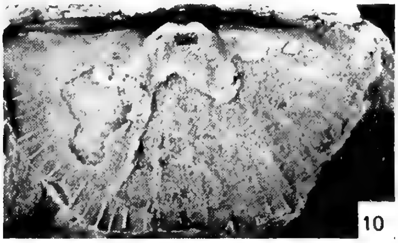
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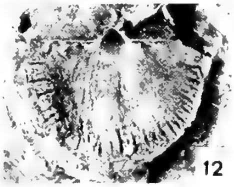
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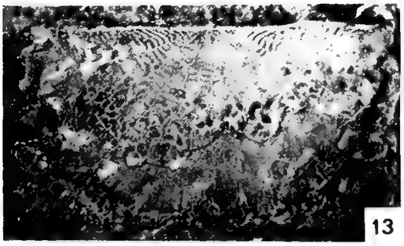
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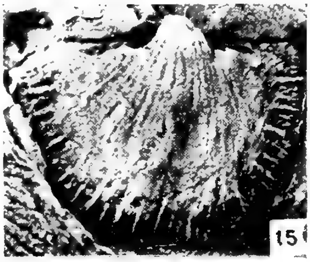
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PLATE 22

Eocramatia dissimulata gen. et sp. nov. (p. 129)

Hope Shales, Brithdir Farm, Shropshire.

FIGS. 1, 2. Paratype, BB 35489a, b. Latex casts of the exterior and interior of a brachial valve, × 5·8.

FIG. 3. Paratype, BB 35492. Latex cast of the exterior of a brachial valve, × 3·4.

FIG. 5. Holotype, BB 35488b. Latex cast of the exterior of a pedicle valve, × 5·3.

FIG. 6. Paratype, BB 35491a. Internal mould of a brachial valve, × 8.

Sowerbyella antiqua Jones (p. 130)

Ffairfach Group, near Llangadog, Carmarthenshire.

FIGS. 7, 4. BB 35525. Latex cast and mould of the interior of a brachial valve, × 11·2, × 7·1.

FIG. 8. BB 35524. Latex cast of the exterior of a brachial valve, × 6·2.

FIG. 9. BB 35530. Latex cast of the interior of a brachial valve, × 4·7.

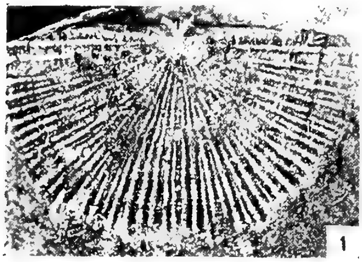
FIG. 10. BB 35529. Latex cast of the interior of a brachial valve, × 8·7.

FIG. 11. BB 35526. Latex cast of the exterior of a brachial valve, × 5·5.

FIG. 12. BB 35532. Latex cast of the interior of a brachial valve, × 6.

FIG. 13. BB 35528. Latex cast of the exterior of a pedicle valve, × 5·5.

FIG. 14. BB 35533. Internal mould of a pedicle valve, × 6.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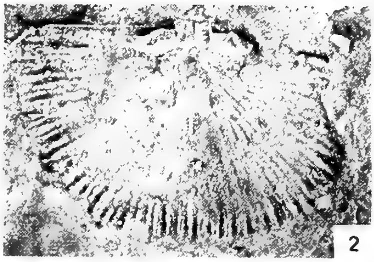
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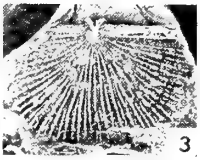
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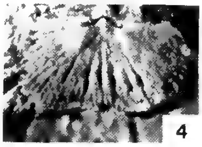
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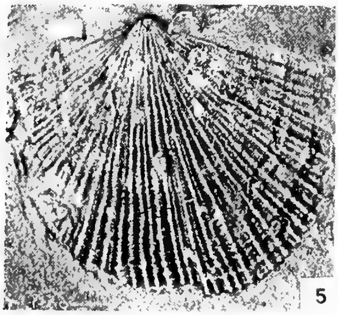
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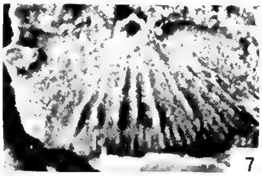
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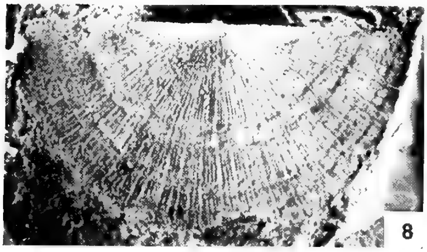
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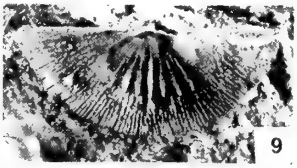
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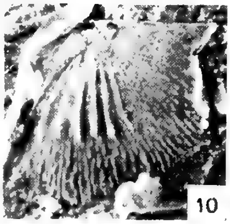
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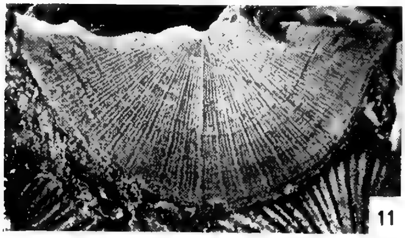
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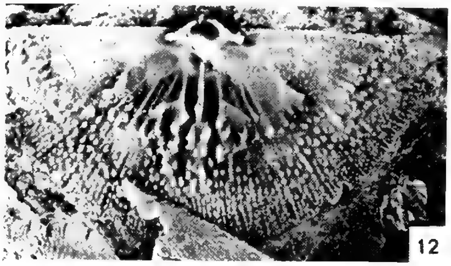
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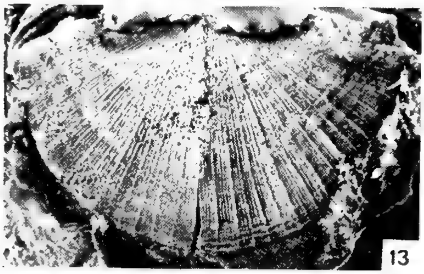
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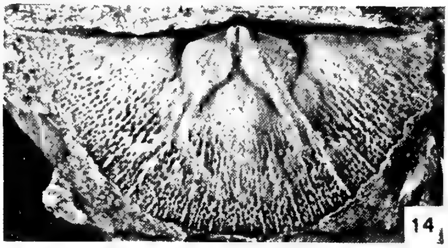
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PLATE 23

Sowerbyella antiqua Jones (p. 130)

Ffairfach Group, near Llangadog, Carmarthenshire.

FIG. 1. BB 35527. Internal mould of a pedicle valve, ×4·7.

FIG. 3. BB 35531. Internal mould of a pedicle valve, ×6.

FIG. 4. BB 35534. Latex cast of the interior of a brachial valve, ×6·5.

Sowerbyella cf. ***antiqua*** Jones (p. 131)

Meadowtown Beds, near Meadowtown, Shropshire.

FIG. 2. BB 35541a. Latex cast of the interior of a brachial valve, ×6.

FIG. 5. BB 35536. Latex cast of the exterior of a brachial valve, ×8·7.

FIG. 6. BB 35539. Internal mould of a pedicle valve, ×6.

FIG. 7. BB 35540. Internal mould of a pedicle valve, ×5·8.

FIGS. 8, 9. BB 35537a, b. Internal mould and latex cast of the exterior of a pedicle valve, ×7·3, ×7·9.

FIGS. 12, 10. BB 35542. Latex cast and mould of the interior of a brachial valve, ×8.

FIG. 11. BB 35535. Latex cast of the exterior of a brachial valve, ×6.

FIG. 13. BB 35538. Internal mould of a brachial valve, ×7.

Sowerbyella multiseptata sp. nov. (p. 132)

Spy Wood Grit, near Rorrington, Shropshire.

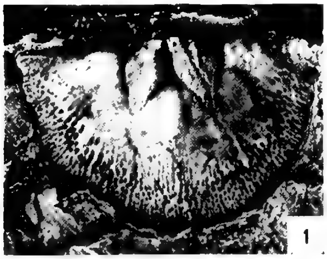
FIG. 14. Paratype, BB 35548b. Latex cast of the exterior of a pedicle valve, ×4·5.

FIGS. 16, 15. Holotype, BB 35544. Latex cast and mould of the interior of a brachial valve, ×6·2.

FIG. 17. Paratype, BB 35547a. Latex cast of the interior of a brachial valve, ×6.

FIG. 18. Paratype, BB 35546a. Internal mould of a pedicle valve, ×7.

FIG. 19. Paratype, BB 35545b. Latex cast of the exterior of a pedicle valve, ×10.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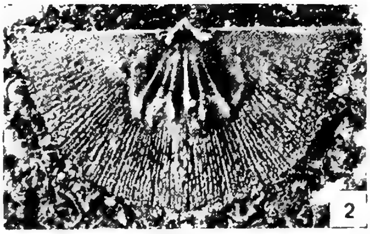
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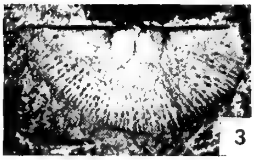
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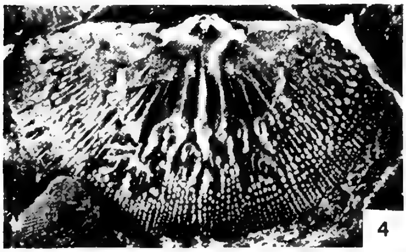
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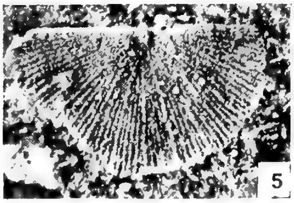
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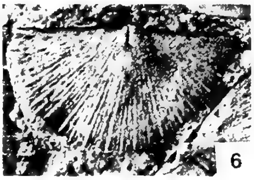
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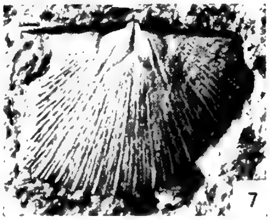
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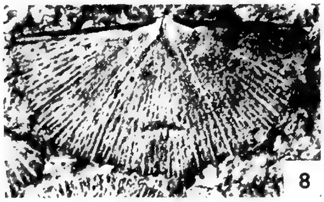
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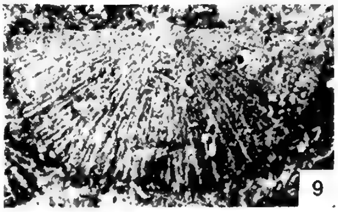
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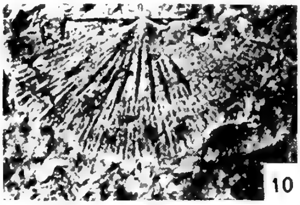
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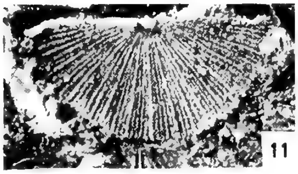
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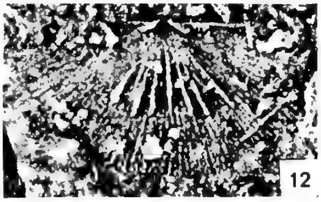
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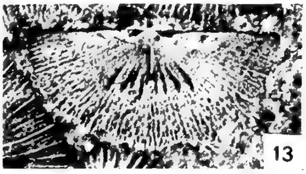
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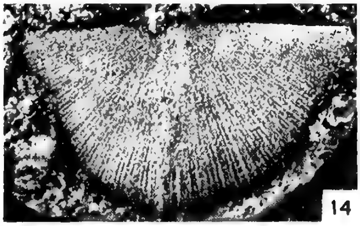
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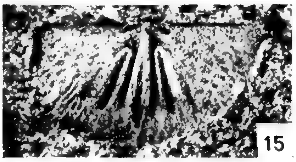
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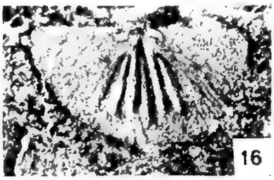
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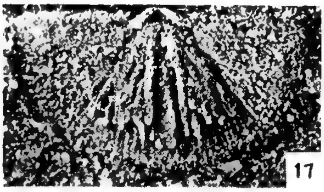
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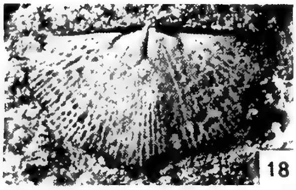
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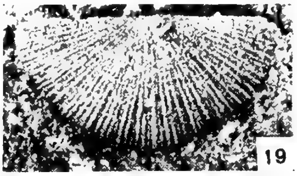
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PLATE 24

Sowerbyella multiseptata sp. nov. (p. 132)

Spy Wood Grit, near Rorrington, Shropshire.

FIG. 1. Paratype, BB 35548a. Internal mould of a pedicle valve, ×6·6.

FIG. 3. Paratype, BB 35545a. Internal mould of a pedicle valve, ×5·8.

Sowerbyella cf. ***sericea permixta*** Williams (p. 133)

Aldress Shales, Ox Wood Dingle, Shropshire.

FIGS. 2, 10. BB 35552a, b. Latex casts of the exterior and interior of a brachial valve, ×6·8.

FIG. 4. BB 35554b. Latex cast of the exterior of a brachial valve, ×5·1.

FIGS. 6, 5. BB 35553a, b. Latex casts of the exterior and interior of a brachial valve, ×4·8, ×5·7.

FIG. 7. BB 35551a. Internal mould of a pedicle valve, ×3·7.

Sowerbyella cf. ***sericea*** (J. de C. Sowerby) (p. 134)

Whittery Shales, near Marrington Farm, Shropshire.

FIG. 11. BB 35555. Internal mould of a pedicle valve, ×3·2.

Whittery Shales, Whittery Wood, Chirbury, Shropshire.

FIGS. 14, 13. BB 35556a, b. Latex casts of the exterior and interior of a brachial valve, ×3·5.

Whittery Shales, near Hockleton Bridge, Shropshire.

FIG. 16. BB 35557. Exterior of the pedicle valve, ×2·7.

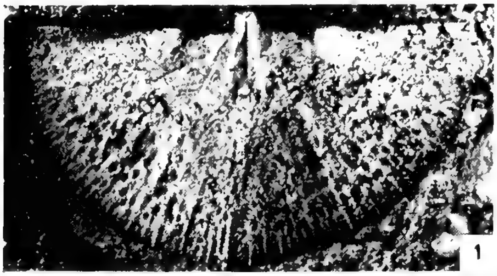
Sericoidea cf. ***abdita*** Williams (p. 139)

Hagley Shales, Church Stoke, Shropshire.

FIG. 8. BB 35485. Latex cast of the interior of a brachial valve, ×7·7.

FIGS. 15, 12, 9. BB 35484a, b. Latex casts of the exterior and interior and the internal mould of a brachial valve, ×8.

FIGS. 18, 17. BB 35487a, b. Latex cast of the exterior and the internal mould of a pedicle valve, ×8·6.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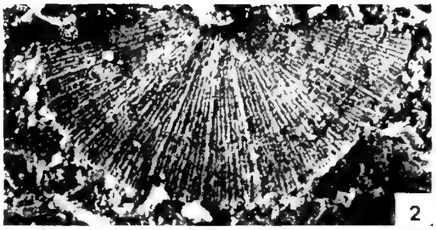
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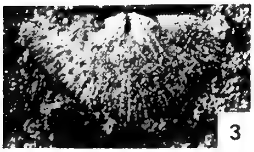
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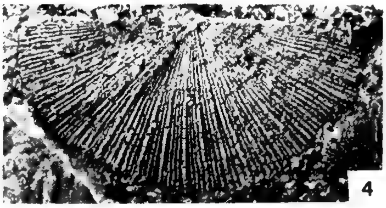
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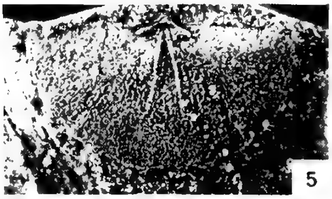
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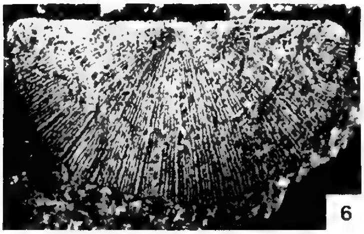
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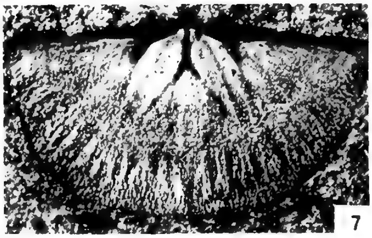
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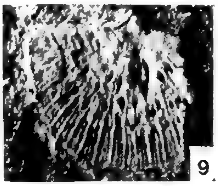
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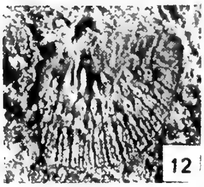
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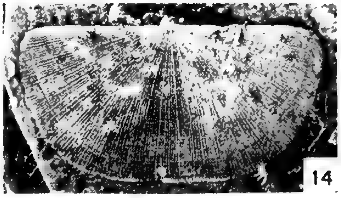
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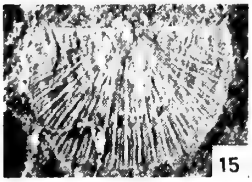
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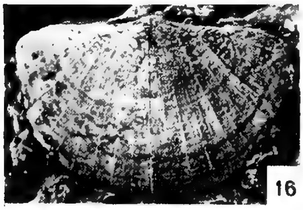
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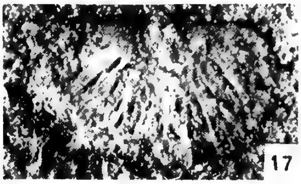
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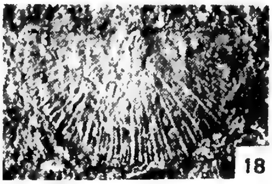
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PLATE 25

Rafinesquina sp. (p. 143)

Whittery Shales, Whittery Quarry, Shropshire.

FIG. 1. BB 35496a. Latex cast of the interior of a brachial valve, ×3.

Murinella sp. (p. 141)

Meadowtown Beds, Little Weston, Shropshire.

FIGS. 2, 3. BB 35421a, b. Latex cast of the exterior and the internal mould of a pedicle valve, ×5, ×4·6.

Furcitella sp. (p. 140)

Whittery Shales, Whittery Quarry, Shropshire.

FIGS. 4, 5. BB 35422a, b. Latex cast of the exterior and the internal mould of a brachial valve, ×4.

Rafinesquina delicata sp. nov. (p. 141)

Meadowtown Beds, Quinton's Quarry, Shropshire.

FIG. 6. Paratype, BB 35562. Latex cast of the interior of a brachial valve, ×2.

FIGS. 8, 7. Paratype, BB 35559a. Latex cast and mould of the interior of a pedicle valve, ×2·6.

FIG. 9. Paratype, BB 35560b. Latex cast of the exterior of a pedicle valve, ×2·9.

FIG. 10. Paratype, BB 35561a. Internal mould of a pedicle valve, ×2·9.

FIG. 12. Paratype, BB 35563a. Latex cast of the interior of a brachial valve, ×3·8.

Meadowtown Beds, near Minicop Farm, Shropshire.

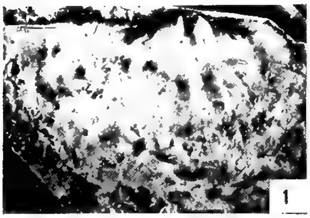
FIG. 11. Holotype, BB 35558a. Internal mould of a brachial valve, ×2·9.

FIG. 13. Paratype, BB 35564b. Latex cast of the exterior of a brachial valve, ×5·4.

Bystromena perplexa gen. et sp. nov. (p. 146)

Spy Wood Grit, near Middleton Church, Shropshire.

FIG. 14. BB 35366a. Latex cast of the interior of a pedicle valve, ×5·6.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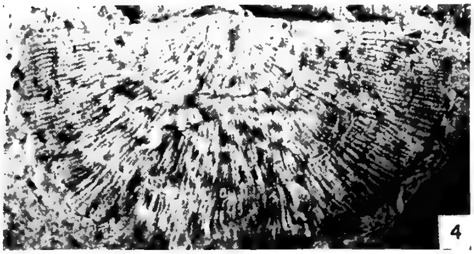
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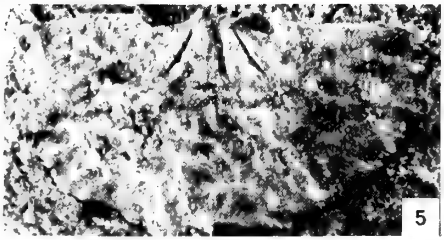
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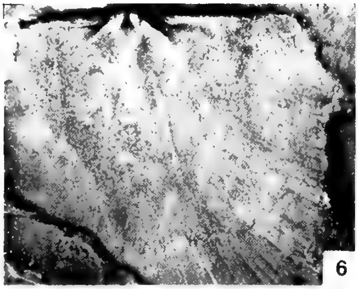
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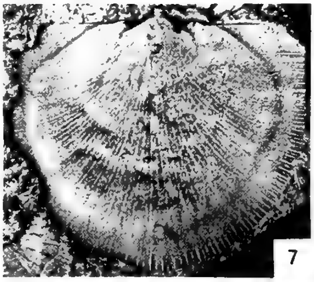
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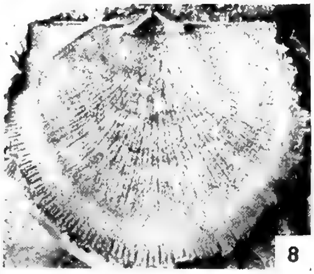
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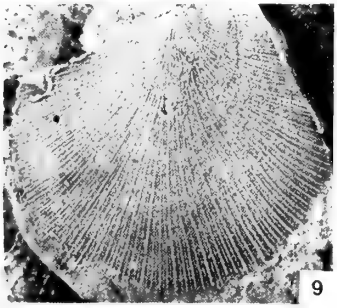
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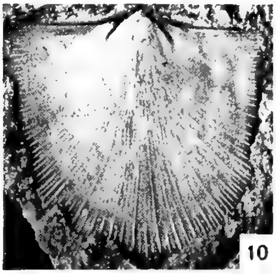
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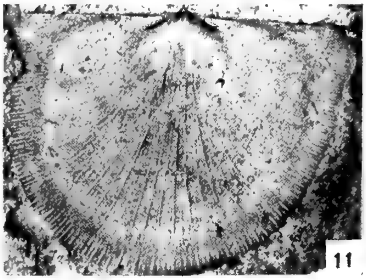
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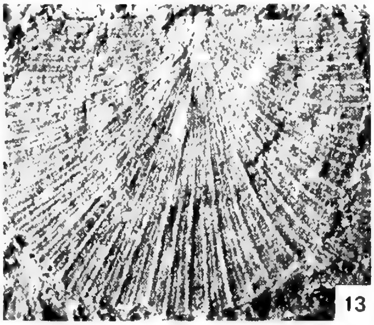
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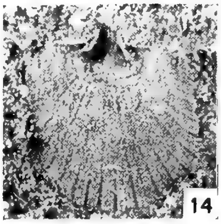
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PLATE 26

Rafinesquina sp. (p. 143)

Whittery Shales, Whittery Quarry, Shropshire.

FIG. 1. BB 35496b. Latex cast of the exterior of a brachial valve, × 5.

Kjaerina (Hedstroemina) sp. (p. 145)

Spy Wood Grit, near Rorrington, Shropshire.

FIG. 2. BB 35452. Internal mould of a pedicle valve, × 1·8.

Bystromena perplexa gen. et sp. nov. (p. 146)

Spy Wood Grit, near Rorrington, Shropshire.

FIGS. 4, 3. Holotype, BB 35363. Latex cast and mould of the interior of a pedicle valve, × 3·4, × 4.

FIGS. 14, 9. Paratype, BB 35365a. Latex cast and mould of the interior of a pedicle valve, × 4·5.

FIGS. 10, 5. Paratype, BB 35364a. Latex cast and mould of the interior of a pedicle valve, × 6·6, × 4·3.

FIGS. 6, 7. Paratype, BB 35370. Latex cast and mould of the interior of a brachial valve, × 7, × 5.

Spy Wood Grit, Spy Wood Brook, Shropshire.

FIGS, 12, 13. Paratype, BB 35368a. Latex cast and mould of the interior of a brachial valve, × 6.

Spy Wood Grit, near Middleton Church, Shropshire.

FIG. 8. Paratype, BB 35367a. Latex cast of the interior of a brachial valve, × 6.

FIG. 11. Paratype, BB 35366a. Internal mould of a pedicle valve, × 7·3.


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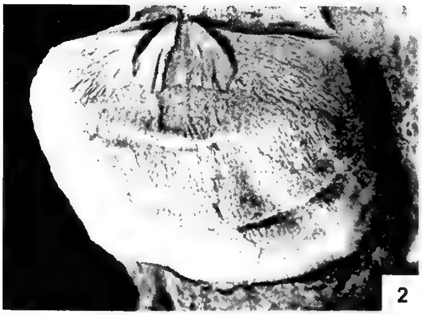
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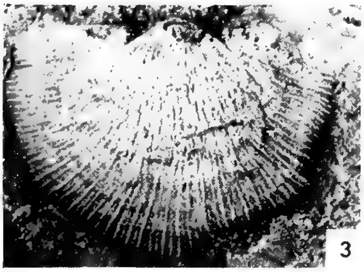
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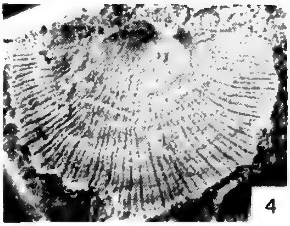
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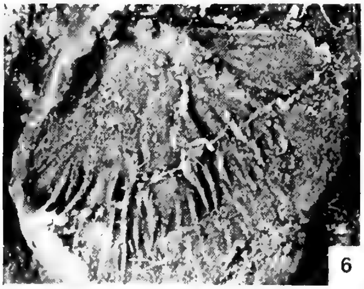
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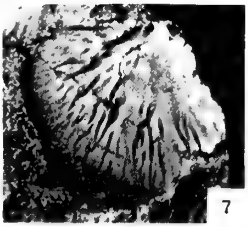
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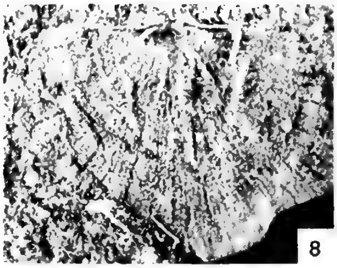
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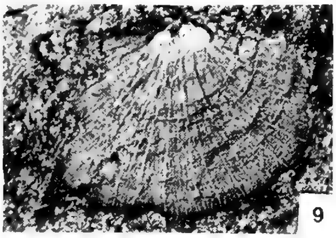
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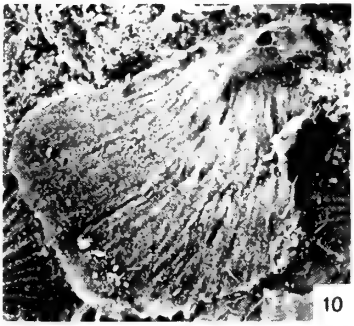
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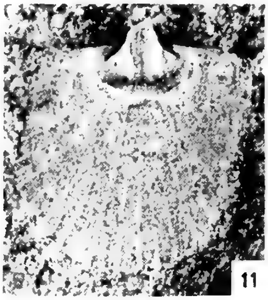
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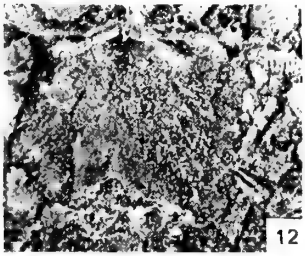
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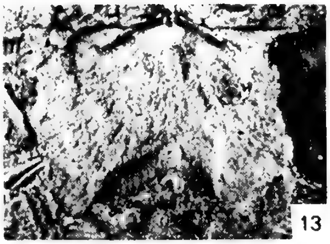
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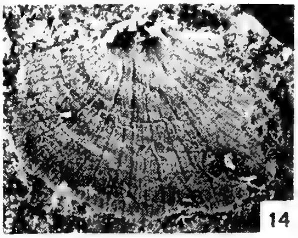
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PLATE 27

Bystromena perplexa gen. et sp. nov. (p. 146)

Spy Wood Grit, near Middleton Church, Shropshire.

FIGS. 2, 1. Paratype, BB 35367a, b. Latex cast of the exterior and the internal mould of a brachial valve, ×7·5.

Rostricellula sparsa Williams (p. 153)

Spy Wood Grit, near Rorrington, Shropshire.

FIGS. 3, 7. BB 35584a, b. Latex cast of part of the exterior and the internal mould of a brachial valve, ×6·9, ×10.

FIG. 4. BB 35585a. Internal mould of a pedicle valve, ×7·5.

Leptaena cf. ***ventricosa*** Williams (p. 148)

Whittery Shales, near Hockleton Bridge, Shropshire.

FIG. 5. BB 35454. Internal mould of pedicle valve, ×2·5.

Whittery Shales, near Marrington Farm, Shropshire.

FIGS. 8, 9. BB 35453a, b. External mould and latex cast of the interior of a brachial valve, ×4, ×3·4.

Kiaeromena cf. ***kjerulfi*** (Holtedahl) (p. 149)

Hagley Volcanics, near Church Stoke Hall, Shropshire.

FIG. 6. BB 37132a. Latex cast of the interior of a brachial valve, ×4·8.

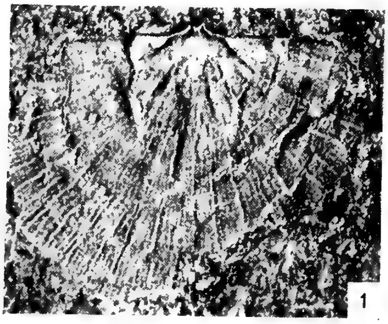
Whittery Shales, River Camlad, Shropshire.

FIGS. 11, 10. BB 35406a, b. Latex cast of the ornament and the internal mould of a pedicle valve, ×6, ×2.

Zygospira sp. (p. 154)

Spy Wood Grit, near Rorrington, Shropshire.

FIGS. 13, 12. BB 37133. Latex cast and mould of the interior of a brachial valve, ×11.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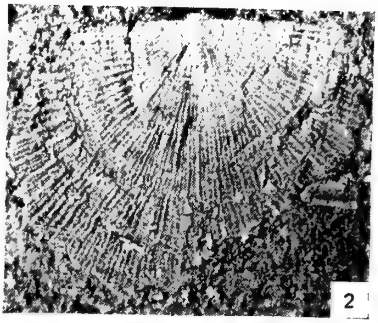
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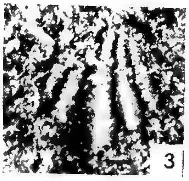
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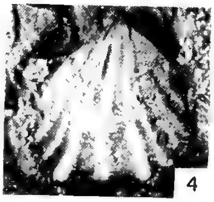
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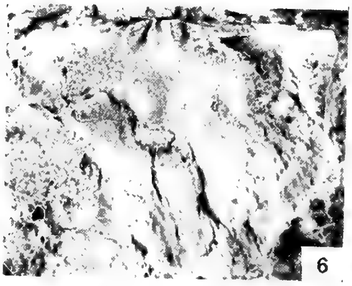
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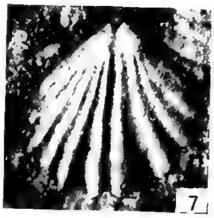
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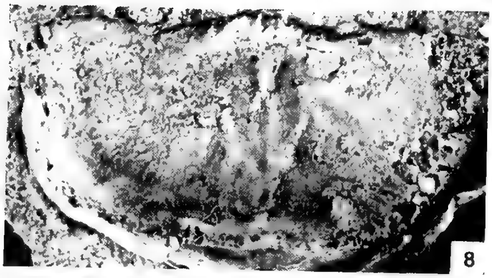
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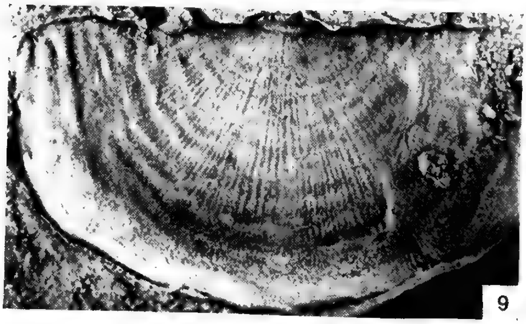
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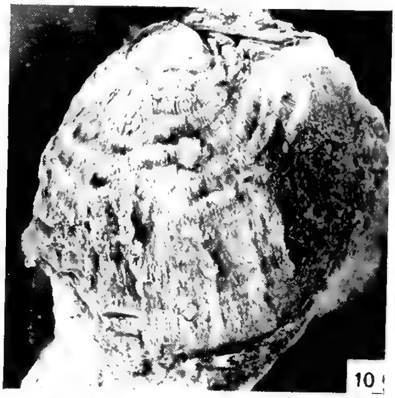
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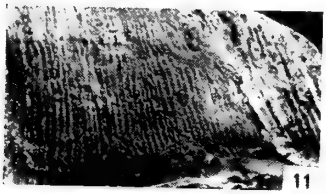
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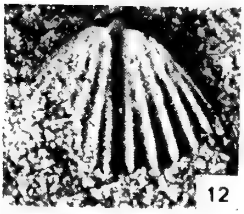
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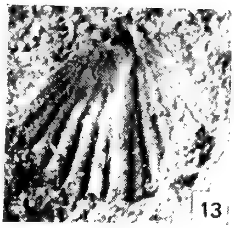
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PLATE 28

Euorthisina* cf. *moesta minor Havlíček (p. 150)

Mytton Flags, near St Luke's Church, Shropshire.

FIG. 1. BB 35377a. Moulds of a group of shells in an orthocone, × 5.
FIG. 5. BB 35377b. Latex cast of the exterior of a brachial valve in the orthocone, × 6.
FIG. 2. BB 35378a. Internal mould of a pedicle valve, × 4·4.

Mytton Flags, near Wood House, Shropshire.

FIG. 3. BB 35379a. Internal mould of a pedicle valve, × 6·3.
FIG. 8. BB 35380a. Internal mould of a brachial valve, × 4.

Euorthisina moesta (Barrande) (p. 150)

Šárka Formation (Llanvirn), Rokycany, Czechoslovakia.

FIG. 4. BB 37160. Dorsal view of the internal mould of a shell, × 1·8.
FIG. 6. BB 37161. Internal mould of a pedicle valve, × 2·4.
FIG. 7. BB 37162. Internal mould of a brachial valve, × 2·5.

Parastrophinella musculosa sp. nov. (p. 151)

Spy Wood Grit, near Rorrington, Shropshire.

FIGS. 9, 17. Holotype, BB 35598a, b. Latex cast of the exterior and the internal mould of a pedicle valve, × 5, × 4.

FIG. 10. Paratype, BB 37108. Internal mould of a brachial valve, × 3·7.
FIG. 11. Paratype, BB 37107. Internal mould of a pedicle valve, × 5·5.
FIG. 12. Paratype, BB 35599a. Internal mould of a brachial valve, × 5.
FIG. 13. Paratype, BB 35600. Internal mould of a brachial valve, × 4·5.

Parastrophinella sp. (p. 152)

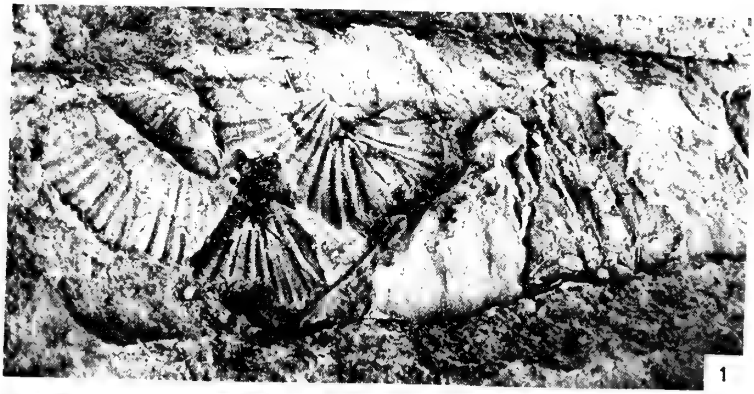
Hagley Volcanics, near Church Stoke Hall, Shropshire.

FIGS. 14, 15. BB 35461a, b. Latex cast of the exterior and the internal mould of a pedicle valve, × 1·8.

Sericoidea* cf. *abdita Williams (p. 139)

Hagley Shales, near Church Stoke, Shropshire.

FIG. 16. BB 35486b. Internal mould of a brachial valve, × 11·5.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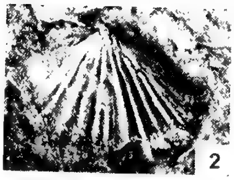
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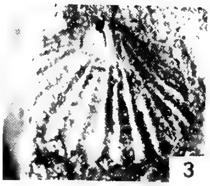
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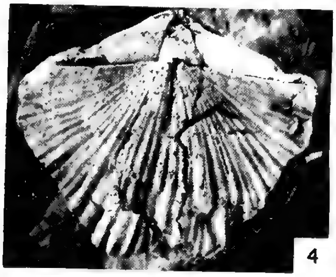
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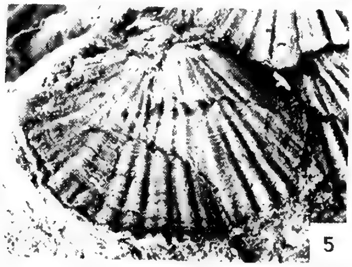
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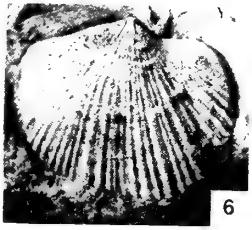
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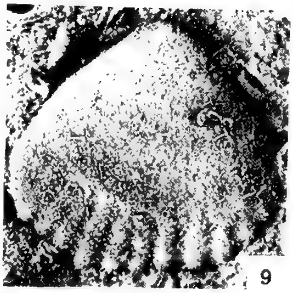
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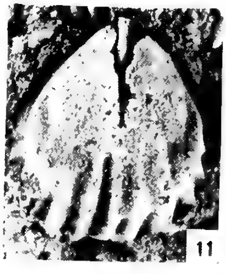
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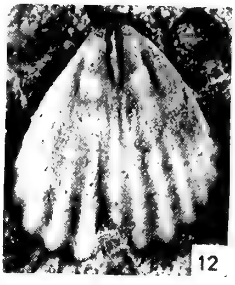
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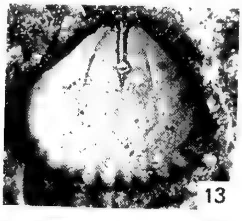
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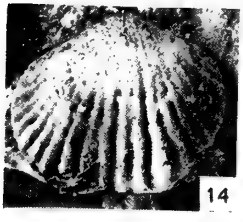
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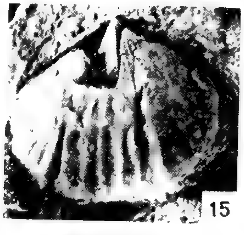
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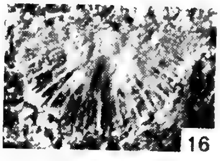
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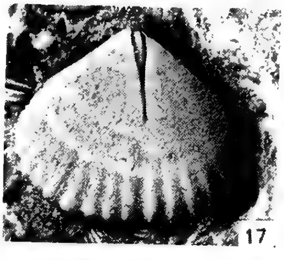
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